RESTORATION AND EFFECTS OF THE WALKER RIVER ENVIRONMENT ON BIOLOGICAL INTEGRITY AND SECONDARY PRODUCTION

Donald W. Sada
Kumud Acharya
Christopher Hogle
Knut Mehler
Christopher Rosamond

Division of Hydrologic Sciences, Desert Research Institute, Reno, NV

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SUMMARY

During the Walker River Phase I studies, BMIs and physicochemical characteristics of the Walker River were sampled during spring, summer, and autumn to determine environmental factors that are most influential to ecological health and structuring the composition of communities. Runoff during these years was less than 50 percent of normal, which biased observations toward drought conditions and prevented assessment of biological and environmental characteristics of the river along a precipitation gradient from drought to wet years. The narrow range of drought environments during these years did not include a gradient of biotic/environmental relationships that is necessary for an unbiased assessment of biotic/environment relationships.

Phase I studies documented that BMI communities change along the gradient of environments from the base of the Sierra Nevada to Walker Lake, and that they are most influenced by low discharge, high temperatures, substrate size, and elevated nutrients. Biotic indices showed a similar pattern where tolerance values for the community were highest downstream and generally decreased along an elevational gradient toward the Sierra Nevada. Communities associated with cooler temperatures, higher discharge, large substrates, and lower nutrient concentrations (low tolerance values) were more similar to those occupying healthy aquatic systems than communities in degraded systems. Higher tolerance communities were associated with areas that are most impacted by agriculture and diversion, but the absence of baseline environmental and biological information describing historical (reference) conditions in this portion of the river make it difficult to discern the relative influence of natural and human factors on these communities. Trends observed during 2007 and 2008 implied, however, that increased discharge, and reduced water temperature and nutrients would improve river conditions and concomitantly beneficially affect aquatic communities (Chandra and Sada [eds.] in Collopy and Thomas 2010). These factors are also influenced by human activity, which suggests that ecological integrity of the Walker River may be affected by activities that alter discharge and thermal regimes, influence substrate composition, and affect nutrient availability. This work provided little insight into ecological benchmarks that can be used to assess restoration efficacy.

Phase II studies were conducted to collect additional information, clarify results of Phase I studies, quantitatively determine secondary production, and provide benchmarks to assess restoration efficacy. Phase II studies consisted of 1) sampling BMIs during a wet year (2010) to assess differences in the community and the river environment during drought years (2007 and 2008) and a year with above average precipitation, and 2) initiating a program to determine the relationship between water temperature and secondary production to increase the understanding of how changes in water temperature may influence trout food. Phase II work provides a basis to: 1) identify the most important environmental factors to be affected by restoration in different

reaches of river, and 2) assess relationships between the river environment and secondary production to determine conditions that support higher trophic levels (i.e., fish populations).

Results of Phase II studies are:

Reference conditions for the upper East Walker River and West Walker River were quantified (collection sites EWC, WWC, WWB). Reducing nutrient loading is important for the East Walker River downstream from Bridgeport Reservoir and upstream from Mason Valley (collection site EWB). The restoration goal for this reach should be to create water quality conditions that maintain a BMI community similar to the community in the upper West Walker River and East Walker River upstream from Bridgeport.

Discharge was higher and water temperatures were lower in 2010 than in 2007 and 2008. As a consequence, characteristics of the upper Mason Valley BMI community (collection site WD) resembled lower East Walker and West Walker communities (collection sites EWA and WWA) during the summer and autumn of 2010. This suggests that EWA and WWA communities occurred downstream into upper Mason Valley prior to anthropogenic influences, and the restoration goal for the this reach of river is create conditions in upper Mason Valley that are similar to those at EWA and EWB.

Identifying restoration goals for the lower Walker River is difficult because reference conditions are difficult to quantify, the magnitude of human influences are greatest in this reach (which potentially limits effects of cooler conditions on the river environment), and there was little difference in BMI communities during drought and above average precipitation years. However, the lowest reach (WA) studied was distinguished by the unique presence of a moderately tolerant BMI species, which is not likely to occur here if conditions in this portion of river are improved. A restoration goal for this reach of river is to improve conditions whereby this species no longer occupies this reach of river.

BMI species richness, density, and biomass are inversely associated with substrate size. Therefore, it is unlikely that productivity in reaches of river with smaller substrate size (e.g. mid-Mason Valley to Walker Lake) can reach levels in reaches of river with larger substrate (e.g., the East Walker River and West Walker River).

Baetis sp. (the most ubiquitous BMI species in the Walker River basin) biomass is negatively associated with temperature. More work is necessary, but it appears that its biomass decreases rapidly in temperatures >12^{o}C.

INTRODUCTION

Prehistoric and historic environmental conditions in the Walker River have varied in response to drought, climate change, and human use. Natural change has been extreme over the past 15,000 years, and included the lower river course changing, Walker Lake drying, and glaciers covering the upper basin (Adams 2007). These changes had demonstrable effects on aquatic life in the basin. The upper basin was historically fishless due to glaciers and aquatic life disappeared from Walker Lake when it dried. River life also changed in response to varying widely varying temperature and precipitation regimes. During cool, moist periods when the lake was watered, Lahontan cutthroat trout inhabited the lake and reaches of river downstream from the mountain block. It was extirpated from lower reaches of river during extended droughts (and when the lake dried) and persisted during these periods near the mountains in reaches of cool streams. This natural variability in climate can be expected to continue and, as in many other rivers, the ecological effects of this variability during drought conditions are likely to be exacerbated by human activity (Beutel et al. 2001). The biological integrity of the Walker River depends on how effectively human uses can maintain an integrated river and lake system that varies within the ecological limits of a healthy ecosystem.

The Walker River is one of three rivers flowing into Nevada from the Sierra Nevada. Historically it supported an important Lahontan cutthroat trout fishery and a diverse series of aquatic systems that ranged from small, cold headwaters to an alkaline terminal lake. The river system has been changed by diversions and impoundments that have reduced river discharge, increased summer time water temperatures, altered the timing and magnitude of runoff events, and lowered the level of Walker Lake. Using water for agriculture has also affected water quality by elevating nutrients and turbidity above historical conditions. These changes may affect aquatic life by modifying the structure of aquatic life from organisms that are relatively intolerant of harsh conditions to organisms that are highly tolerant of harsh conditions. Acquiring water to increase the level of Walker Lake will increase river discharge and it should improve lake and riverine environments and life that require high quality conditions.

Physical, chemical, and hydrological characteristics of streams and rivers are the environmental factors that influence their aquatic life (Strange et al. 1999, Lytle and Poff 2004), which has been demonstrated by many studies examining benthic macroinvertebrate (BMI) communities (e.g. Rosenberg and Resh 1993, Barbour et al. 1999). Since this life is specifically adapted to existing conditions, environmental change influences the characteristics of aquatic communities. Their composition changes quickly in response to environmental conditions and the magnitude of its influence on river health can be readily assessed. Much of the work developing these assessments has occurred in mesic regions of North America where environments are benign compared to streams in lower parts of the western Great Basin in Nevada. Little is known about benchmarks for these aquatic systems where communities occupy naturally harsh environments created by high summer temperatures and low base flow.

During our Walker River Phase I studies, BMIs and physicochemical characteristics of the Walker River were sampled during spring, summer, and autumn to determine environmental factors that are most influential to ecological health and structuring the composition of communities (see Collopy and Thomas 2010). Runoff during these years was less than 50 percent of normal, which biased observations toward drought conditions and prevented assessment of biological and environmental characteristics of the river along a precipitation gradient from drought to wet years. The narrow range of drought environments during these years did not include a gradient of biotic/environmental relationships that is necessary for an unbiased assessment of biotic/environment relationships.

These studies documented that BMI communities change along the gradient of environments from the base of the Sierra Nevada to Walker Lake, and that they are most influenced by low discharge, high temperatures, substrate size, and elevated nutrients. Biotic indices showed a similar pattern where tolerance values for the community were highest downstream and generally decreased along an elevational gradient toward the Sierra Nevada. Communities associated with cooler temperatures, higher discharge, large substrates, and lower nutrient concentrations (low tolerance values) were more similar to those occupying healthy aquatic systems than communities in degraded systems. Higher tolerance communities were associated with areas that are most impacted by agriculture and diversion, but the absence of baseline environmental and biological information describing historical (reference) conditions in this portion of the river make it difficult to discern the relative influence of natural and human factors on these communities. Trends observed during 2007 and 2008 imply, however, that increased discharge, and reduced water temperature and nutrients would improve river conditions and concomitantly beneficially affect aquatic communities (Chandra and Sada [eds.] in Collopy and Thomas 2010). These factors are also influenced by human activity, which suggests that ecological integrity of the Walker River may be affected by activities that alter discharge and thermal regimes, influence substrate composition, and affect nutrient availability.

The quality and amount of secondary productivity as a food source for higher trophic levels plays a central role in determining community structure and biogeochemical dynamics in stream ecosystems (Finlay 2011). Due to the strong role of resource availability in ecological structure and dynamics, understanding of natural variation and anthropogenic impacts on production at the base of stream food webs is fundamentally important (Finlay 2011). The production of each trophic level determines the amount of energy and material and consequently the productivity of higher trophic levels (Schoenly et al. 1991, Schindler and Scheurell 2002). Assessing secondary production has become a powerful tool to assess ecosystem structure and functioning and overall ecosystem productivity (Huryn and Wallace 2000). In general, secondary production refers to the formation of animal biomass during time and area ($mass \cdot area^{-1}$), and production is the accrual of biomass of an organism or a population over a certain time period per unit area ($mass \cdot area^{-2} \cdot time^{-1}$). The production/biomass ratio (P/B) provides a means to compare growth rates of species in different communities and populations. Secondary production can then be related to critical stream properties, such as community structure, nutrient cycling rates, and support for higher trophic levels (Wootton and Power 1993, Mulholland et al. 1997). Because the life history patterns of an organisms depends on biotic and abiotic factors, secondary production also reflects the relationship between populations and their environment and is an excellent indicator for ecosystem changes due to natural or anthropogenic disturbances (Butler 1984, Wallace et al. 1982, Leeper and Taylor 1998). In undisturbed streams, secondary production increases downstream along a longitudinal gradient caused by changes in stream size, energy processing, resource availability, and temperature (Vannote et al. 1980). However, anthropogenic impacts can alter this longitudinal relationship. The responses to changes in secondary production on ecosystems processes are complex and not fully understood. On the one hand, an increase in secondary production is expected to increase nutrient uptake and growth of fish and top predators. On the other hand, anthropogenic impacts can alter community composition and favor the abundance of taxa tolerant of degraded habitat conditions. Alterations in community structure attributed to human factors are in turn expected to offset increased production for higher trophic levels by increasing the amount of unpalatable taxa and consequently reducing the production available to top predators (Wootton and Power 1993, Davis et al. 2010). A greater understanding of anthropogenic impacts on secondary production is necessary to fully understand implications for higher trophic levels and other ecosystems services. Secondary production in streams in semi-arid regions, particularly related to anthropogenic induced alterations, is poorly understood (e.g., Jackson and Fisher 1986, Gaines et al. 1992), and a comprehensive study including BMI community composition and secondary production is not available for Walker River. This information however, is essential to assess, which parts of the river are more or less affected by human activities, particularly with regard to the diverse fish populations in the upstream parts of the river (Sada 2000).

Objective and Significance

The objective of our Phase I and II studies was to provide information to guide Walker River restoration by understanding processes that link characteristics of aquatic life and the river environment. Phase I studies provided some insight into this relationship, and Phase II studies were conducted to collect additional information clarify results of Phase I studies and quantitatively determine secondary production. Phase II studies consisted of 1) sampling BMIs during a wet year (2010) to assess differences in the community and the river environment during drought years (2007 and 2008) and a year with above average precipitation, and 2) initiating a program to determine the relationship between water temperature and secondary production to increase the understanding of how changes in water temperature may influence trout food. Phase II work provides a basis to: 1) identify the most important environmental factors to be affected by restoration in different reaches of river, and 2) assess relationships between the river environment and secondary production to determine conditions that support higher trophic levels (ergo fish populations).

METHODS

Site Description

Walker River headwater form streams flow off the Sierra Nevada and form the East and West Walker rivers that combine to the Walker River near Yerington, Nevada (Figure 1). The length of river from its headwaters to its terminus at Walker Lake is approximately 250 km (160 mi). Both forks of the river are free-flowing before entering Antelope (West Walker) and Bridgeport valleys (East Walker) where they are diverted into low-gradient irrigation ditches. Only sites EWC, WWC, and WWB are unaffected by diversion or upstream influences of agriculture. These appear to be reference sites for the river near the base of the Sierra Nevada. The river hydrograph is also altered by Bridgeport Reservoir (East Walker) and Topaz Lake (West Walker) that impound water for agriculture in Mason Valley. Low gradients, slow water, and small substrates characterize valley reaches of both forks, and both forks cascade off of the Sierra Nevada and through steep, narrow canyons where they transition between valleys. River volume increases from melting snow in the spring time and usually peaks in May or June. Flows are typically the lowest from November through February. Average inflow to Walker Lake was estimated to be 76,000 acre-feet by Thomas (1995). Sample sites for this study were selected to represent the variety of river environments in the Walker River and the East and West Forks. All sites were located close to and downstream of USGS stream gauges (except sites WC and WD that were located in ungauged reaches in the center of Mason Valley; discharge at these sites was calculated from depth and velocity measurements during sampling or interpolation from nearby gauges).

Sample Methods

Physicochemical Environment and BMI Community

Physical and chemical environments and BMIs in the Walker River were sampled at sites shown in Figure 1 at seasons and years shown in Table 1.

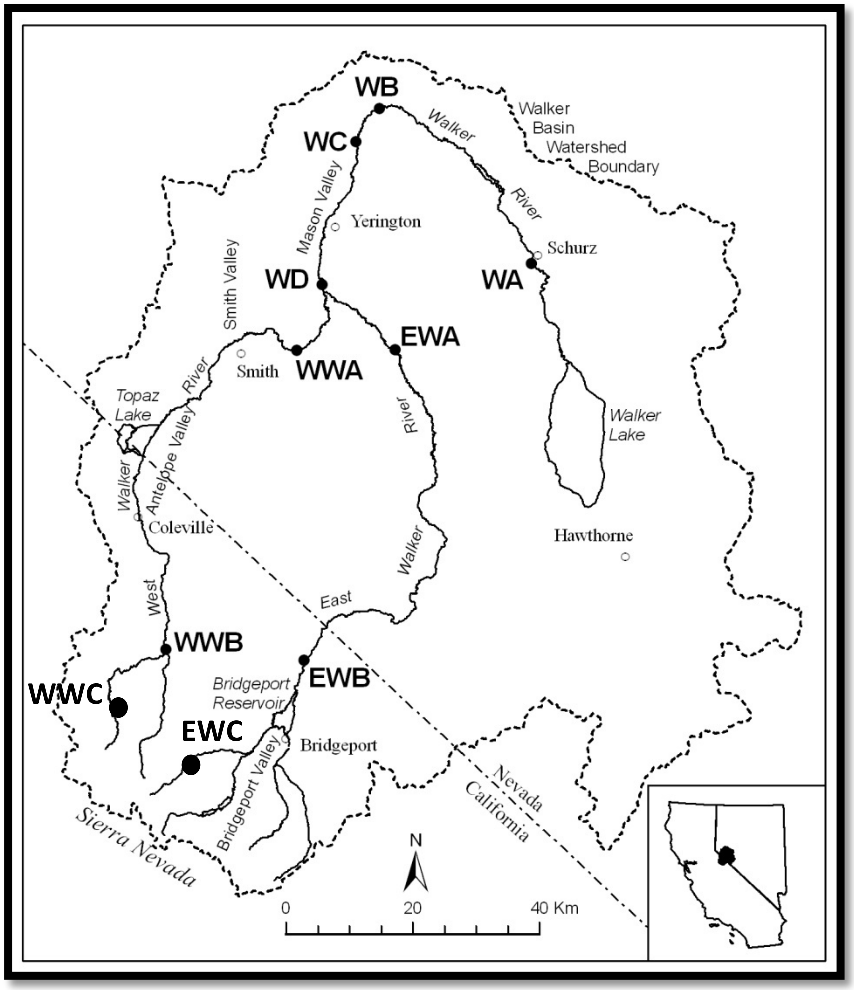

Figure 1. Walker River Basin and the location of 2007, 2008, and 2010 BMI, water chemistry, and physical habitat sampling sites. WA, WB, WC and WD = Walker River sites, EFA and EFB = East Walker sites, and WWA , WWB, and WWC = West Walker sites.

Table 1. Walker River sites, site codes (see Figure 1), elevations, and seasons and years that BMIs and river environments were sampled in 2007, 2008, 2010. SP = Spring, SU = Summer, AU = Autumn.

Sample Site	Reach Code	Elevation (m)	Seasons Sampled	Years Sampled
Walker A	WA	1251	SP (not 2008), SU, AU	2007, 2008
Walker B	WB	1310	SP (not 2008), SU, AU	2007, 2008
Walker C	WC	1320	SP, SU, AU	2007, 2008, 2010
Walker D	WD	1335	SP, SU, AU	2007, 2008, 2010
East Walker A	EWA	1394	SP, SU, AU	2007, 2008, 2010
East Walker B	EWB	1935	SP, SU, AU	2007, 2008, 2010
East Walker C	EWC	2183	SU (not 2008), AU	2008, 2010
West Walker A	WWA	1417	SP, SU, AU	2007, 2008, 2010
West Walker B	WWB	2008	SP, SU, AU	2007, 2008, 2010
West Walker C	WWC	2175	SU, AU	2010

River Environment

Physical and chemical characteristics of the river environment were sampled to quantify features that are most important to BMIs. Environmental variables measured, estimated, and used in BMI community analyses are shown in Table 2. Physical habitat characteristics were determined along transects that spanned the wetted width, and included 25 depth and mean water column velocity measurements at evenly-spaced intervals across each transect using a top-setting wading rod and a Marsh-McBirney Model 2000 flow meter. Substrate size and embeddedness, and the depth of submerged vegetation and detritus were also measured at 100 points along each transect at the four corners surrounding a 1 ft^2 area that was centered on each depth/velocity point. Water temperature was measured at 15 minute intervals from March through September using Hobo® Water Temp Pro Loggers. Some loggers were lost due to vandalism or high flows. In these cases temperature was estimated by regression of nearby weather station data (http:\\www.wrc.dri.edu) and water temperature at upstream sites or ambient air temperature depending on which relationship provided the greatest R^2. All temperature regressions had R^2 values greater than 0.9. Water samples were also collected during BMI sampling and habitat surveys (Table 2). Samples were chilled and returned to the Desert Research Institute Analytical Chemistry Laboratory where total phosphorus, total nitrogen, $NO_2 + NO_3$, and total suspended sediments concentrations were measured following standard methods.

Table 2. Physical and chemical environmental parameters measured during each Walker River BMI sample during 2007, 2008, and 2010. Parameters used in CCA analysis shown in bold. Codes are abbreviations used in CCA. Units of measure are; m = meters, cm = centimeters, mm = millimeters, m/s = meters per second, % = percent, °C = degrees centigrade, mg/L = milligrams per liter.

Habitat Variable	Code	Units
Season	SEASON	Categorical
Elevation	ELEV	m
Wetted Width	WW	m
Mean Water Depth	MnWD	cm
Mean Substrate Size	MnSUB	mm
Fines	F	%
Sand	SA	%
Gravel	GR	%
Cobble	CO	%
Boulder	BO	%
Aquatic Vegetation	VEG	%
Detritus	DETR	%
Mean Embeddedness	MnEmb	%
Mean Water Velocity	MnWV	m/s
Maximum Water Temperature 60 days	MaxT60	°C
Minimum Water Temperature 60 days	MinT60	°C
Total Phosphorus	TP	mg/l
Nitrate + Nitrite	NO_3+NO_2	mg/l
Total Nitrogen	TN	mg/l
Total Suspended Solids	TSS	mg/l

Benthic Macroinvertebrate Samples

The BMIs were collected in six one ft^2 kick-net samples (spaced evenly across the wetted width) along each physical habitat transect, combined into a single composite sample, preserved in 90 percent ethyl alcohol, and returned to the laboratory for processing. In the laboratory, composite samples were sub-sampled by plankton splitter and BMIs identified to the lowest taxonomic level possible, which was to genus for most groups. Approximately 300 randomly selected organisms were identified from each sample. Organisms that could not be identified to the same taxonomic level as other organisms within a taxonomic group were considered ‘non-distinct’ and not used in the analysis. Non-distinct organisms were generally early instars or damaged specimens. Counts of all species were standardized to 300 for each sample. Rare taxa were defined as all taxa that did not total more than 50 organisms in all samples combined, or more than 5 percent (>15 organisms) of any one sample after the counts were standardized to 300. Rare taxa were not used in the analysis. The BMIs collected for secondary production assessment were placed in a white pan after collection, identified to the lowest possible taxonomic level, and individual body lengths were taken immediately in the field by using a microscope. Individual organisms were then placed in vials, kept on dry ice for transport to the laboratory, and stored in the freezer at -20°C until analyzed.

Analytical Methods

A common goal of community analysis is to determine environmental factors that are most important to the animal or plant community being studied, and to identify species that are most indicative of environmental conditions. In watersheds that have not been well studied, such as the Walker River and other watersheds of the western Great Basin, a greater understanding of aquatic communities and ecological gradients is needed to effectively assess biotic integrity and river health (Kennedy et al. 2000). This information is also needed to inform restoration goals, design, and assessment. We analyzed Walker River BMI communities, the river environment, and their seasonal and inter-annual shifts using the biotic Hilsenhoff Biotic Index (HBI) (Hilsenhoff 1988), canonical correspondence analysis (CCA) (ter Braak and Verdonschot 1995), and indicator species analysis (ISA) (Dufrêne and Legendre 1997).

Hilsenhoff Biotic Index

The HSI assigns values to each species that indicate its tolerance to harsh or polluted conditions, and calculates a community tolerance index by prorating the abundance of each species in the community (Hilsenhoff 1981, Karr 1999). Communities in polluted or harsh environments are indicated by high HSI values and low values are indicative of communities in high quality environments.

Canonical Correspondence Analysis

The CCA is a multivariate analysis that provides insight into the environmental factors that most affect the structure of BMI communities (ter Braak and Verdonschot 1995). Results were calculated by PC-ORD v. 6.0 (McCune and Grace 2002) and plotted optimizing samples and using biplot scaling. The first three axes of variation were interpreted and the significance of the first axis was tested using 999 Monte Carlo tests of randomized data. Sites WWC and EWC were not included in CCA to minimize total variation and focus the analysis of environmental eigenvectors on parts of the watershed of primary interest for restoration. The BMI data consisted of counts of each species standardized to a count of 300 individuals. Proportional data (ergo each substrate type, sample points with vegetation and detritus, and substrate embeddedness) were categorized into 12 classes to avoid violation of covariate assumptions (1 < 1%, 3 =1 - 4.9% 10 = 5 - 14.9%, 20 = 15 - 24.9%, 30 = 25 - 34.9%, 40 = 35 - 44.9%, 50 = 45 - 54.9%, 60 = 55 - 64.9%, 70 = 65 - 74.9%, 80 = 75 - 84.9%, 90 = 85 - 94.9%, 98 > 95%). All other environmental variables were values that were measured during sampling. Only environmental variables with eigenvectors $\geq R^2 = 0.300$ were plotted.

Indicator Species Analysis

The ISA is an assessment that groups or clusters communities according to similarities in their structure, and identifies species with greatest fidelity to each group (Dufrêne and Legendre 1997). Because there is a strong relationship between river environments and the structure of BMI communities, groups identified by this analysis are associated with distinctive Walker River environmental characteristics. Additionally, ISA identifies indicator species and calculates an indicator value (IV) that ranks the relative abundance and consistency of each indicator species for a group. These values range from 0 (no indication of association to a group) to 100 (perfect association). The ISA was conducted using *PC-ORD* v. 6 (McCune and Grace 2002) to examine 2007, 2008, and 2010 samples. Rare species were excluded from analysis. There are strengths and limitations to each of these analyses in context of restoration, and benthic community datasets on a watershed scale are often characterized by high dimensionality due to the large number of taxa in the data set (Miserendino 2001). To maximize the utility of BMI and river environment information to develop restoration goals and programs, we integrate results of HBI, CCA, and ISA. Tetra Tech (2007) calculated biotic indicies for lower portions of the Truckee, Carson, and Walker rivers and concluded that existing biotic indices based largely on HBI (Hisenhoff 1988) and EPT (the prorated proportion of insect orders Ephemeroptera, Plecoptera, Trichoptera in the BMI community) diversity cannot accurately describe river health for lower watersheds due to the difficulty establishing indicies when reference conditions are poorly understood (e.g., Blinn and Ruiter 2006, Stoddard et al. 2006). The utility of singular use of CCA is limited because it identifies environmental factors that are important to structuring BMI communities, but it graphically represents information in two or three dimensions that may be insufficient to accurately represent community structure (McCune and Grace 2002). The ISA groups similar communities but provides little insight into environmental factors that are relevant for each group. Considering results from each of these analyses provides an integrated assessment of benthic life in the Walker River and environmental factors that are most important to structuring its communities.

Benthic Macroinvertebrate Secondary Production

The BMIs used to examine secondary production were thawed, dried at 50°C for 72 h and the individual body mass of the dried organisms was determined to the nearest 0.1 mg. Together with the individual body length, length-mass-relationships were developed for each sampled taxa.

In case of a low abundance of a species, length-mass-relationships cannot be developed; conversion factors for these species were taken from the literature (e.g. Benke et al. 1999). The size frequency distribution (Hynes and Coleman 1968) was applied to the most common species (e.g. *Baetis* spp.) by categorize them into size classes. For each size class the average cohort density (g/m^2) was calculated to obtain a size frequency distribution known as an average cohort.

The change in density of each cohort was used to estimate the survivorship of an average cohort. The production of each cohort was then calculated as the net change in mean annual density and the mean individual biomass between size classes (Table 3). Cohort production P is the sum of the last column, and annual P/B (production/biomass ratio) is equal to the sum of cohort P divided by sum of cohort B, assuming development time is one year. Because most of the taxa deviate from a one year development time, a correction factor must be applied to the sum of the last column, which involves the multiplication by the yearly time (12 months) interval/CPI (Cohort Production Interval). CPI is the mean development time of a population from hatching to final size and can be estimated for each species. Therefore, annual production P can be calculated as 12/CPI (Σ cohort P). That value was taken to calculate the annual P/B ratio.

Table 3.Variables and equations to calculate secondary production and turnover ratios using the size frequency method, exemplified for 3 size classes (after Hynes and Coleman 1968).

Length	Density	Individual Mass	Number Lost	Biomass	Mass at Loss	Biomass Lost	Cohort Prodcution
mm	No/m^2	mg	mg	mg/m^2	mg	mg/m^2	mg/m^2/time period
1	X1	Y1		X1 x Y1			
2	X2	Y2	X2-X1	X2 x Y2	(Y1+Y2)/2	(Y1+Y2)/2 x X2-X1	((Y1+Y2)/2 x X2-X1)) x3
3	X3	Y3	X3-X2	X3 x Y3	(Y2+Y3)/2	(Y2+Y3)/2 x X3-X2	((Y2+Y3)/2 x X3-X2)) x3
				Biomass B = Σ			Cohort P = Σ

RESULTS

A total of 25,250 individual BMIs were identified from 342 taxa in 69 samples. Many of these taxa rarely occurred in samples. Rare taxa were defined as all taxa that did not total more than 50 organisms in all samples combined, or more than 5 percent (>15 organisms) of any one sample after the counts were standardized to 300. Rare taxa were not used in CCA or ISA due to the relatively large influence of rare taxa on the results of these analyses. A total of 907 animals belonging to 37 taxa were analyzed to estimate secondary production.

Hilsenhoff Biotic Index

The HBI increased along a gradient from upstream to downstream (Figure 2). This tolerance gradient was associated with increasing anthropogenic disturbance downstream, but may also have been influenced by a covariate trend in elevation and water temperature. Sites WWB, WWC, and EWC were minimally influenced by human activities. Similarities between their HBIs and their occurrence at similar elevations in different sub-drainages suggests these sites can be considered as ‘reference’ for the East and West Forks at the base of the Sierra Nevada. Our data provide little insight into reference conditions from lower Mason Valley to Walker Lake because there are no areas that are unaffected by diversion and agriculture (e.g., Poff 1997, Ciesielka and Bailey 2007).

Variability among samples is relatively consistent between reaches, except for sites WD, EWB, and EWC. Variability at WD was greater than other reaches largely due to an uncharacteristically low HBI index (2.5) observed during the 2010 summer when water temperatures were low due to higher discharge from greater than average winter precipitation. The range in HBI values during all other WD samples was from 6.1 to 7.4. Tolerance values at EWB and EWC were consistently lower than most other sites, and variability for EWB ranged from 4.8 to 5.4 and for EWC it was 4.0 during each survey.

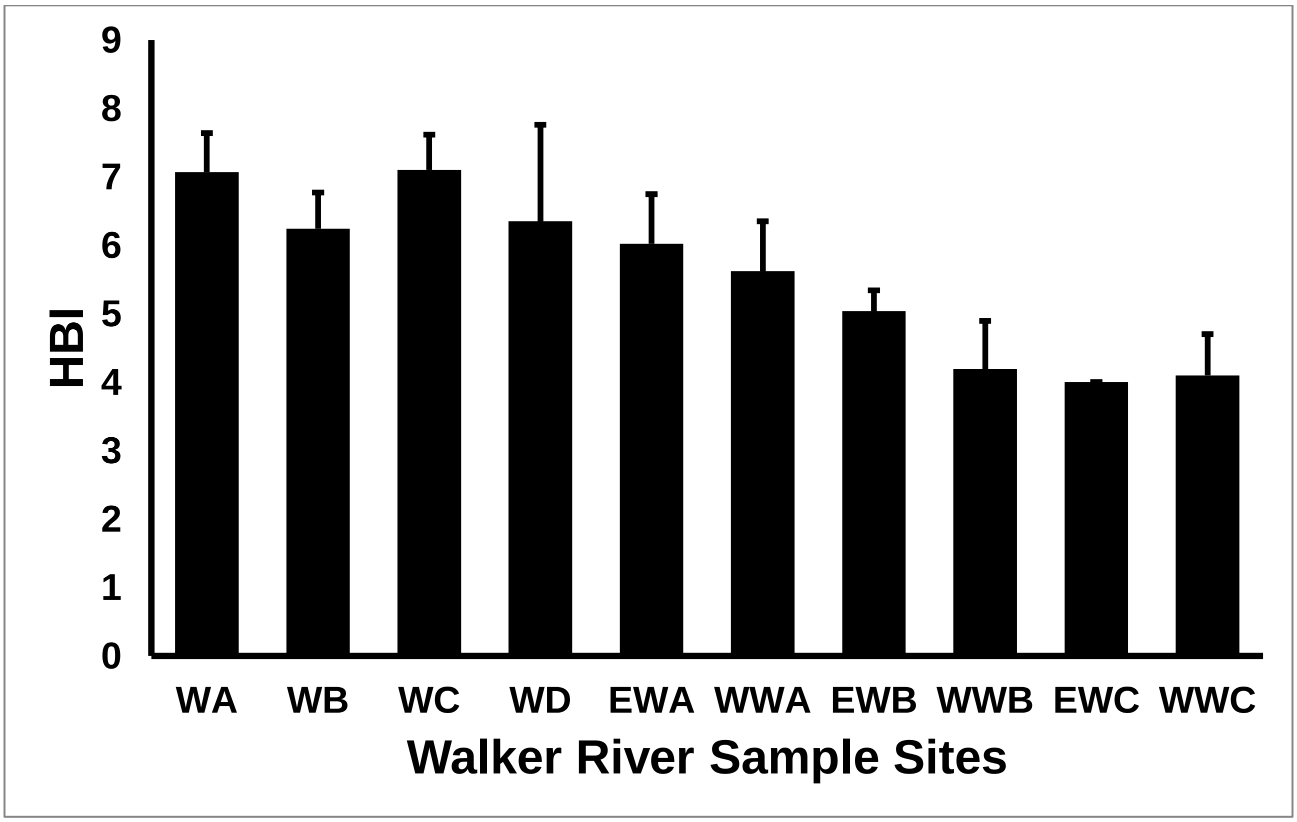

Figure 2. Grand mean Hilsenhoff Biotic Index (+ 1 standard deviation) for all Walker River BMI collection localities during 2007, 2008, and 2010 organized sequentially from the lowest elevation (WA) to the highest elevation (WWC) sites.

Canonical Correspondence Analysis

The CCA examined relationships between 69 species and 20 environmental variables for 64 samples. Rare taxa were not used in the analysis and the species matrix was LOG(n+1) transformed to stabilize variance. A biplot of the results shows relationships between BMI communities during each sample and reach of river (polygons) relative to important environmental factors (Figure 3). Axis 1 had a significant (p = 0.01) eigenvalue of 0.318 and was generally associated with geomorphic (i.e., cobble, sand, embeddedness, sand, fines) and elevation/temperature related (i.e., elevation, maximum temperature) variables. Axis 2 had an eigenvalue of 0.193 and was primarily associated with nutrient related variables (i.e., total nitrogen, total phosphorus, NO_3+NO_2). Axis 3 (not shown) had an eigenvalue of 0.142 and was primarily associated with season and temperature. Samples largely grouped by site in the biplot, suggesting there was often substantial similarity of BMI communities at each site. Although the CCA ordination biplot showing Axis I and II was not representative of the full range of community variation (ter Braak and Verdonschot 1995) it effectively illustrates the relative contribution of the measured habitat variables in structuring the community groupings calculated by the ISA. These results also suggest that factors influencing nutrients, water temperature, and substrate may be the most important parameters to be considered during river restoration.

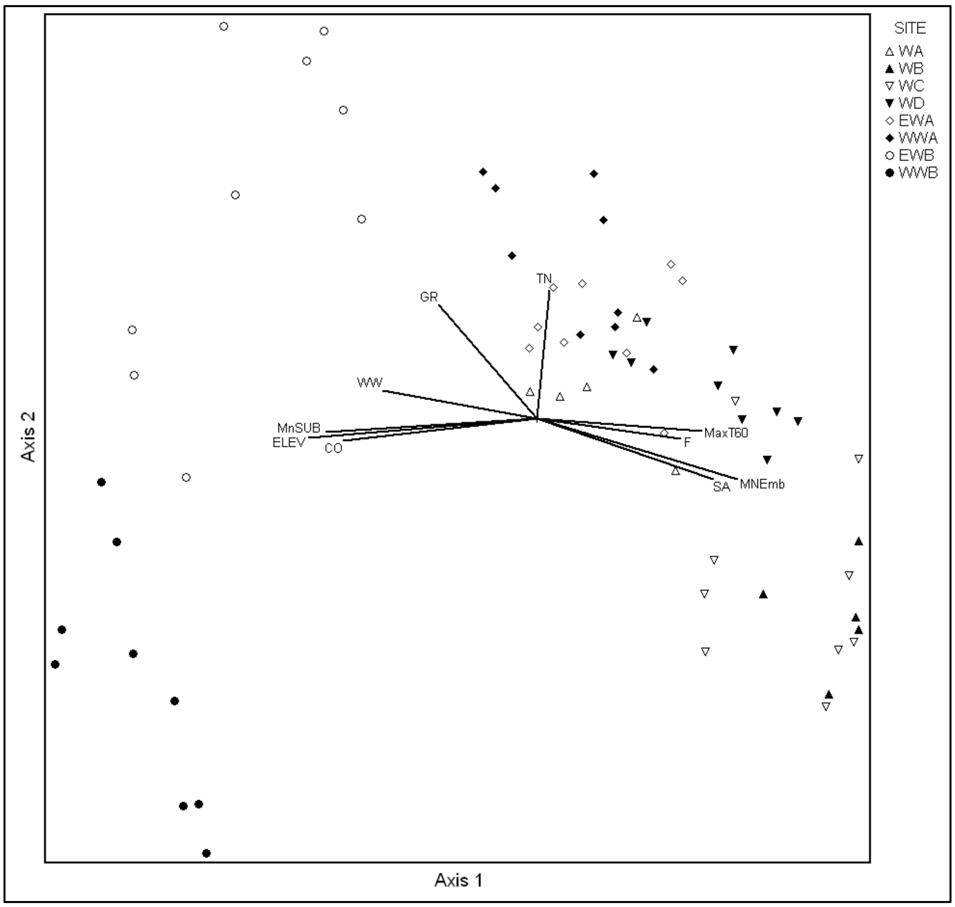

Figure 3.A CCA biplot showing sample sites and statistically significant ($p < 0.05$) environmental variables structuring the Walker River BMI community. Sample sites as abbreviated in Table 1.

Indicator Species Analysis

The ISA analyzed 69 taxa in 69 samples. A dendrogram created from a Bray-Curtis cluster analysis graphically summarizes ISA results, and illustrates groupings in a step-wise manner by hierarchically clustering samples according to similarities in community composition (Figure 4). Samples (i.e. BMI communities) were grouped seasonally and along the gradient from headwaters to the lower river (Figure 4, along left side of chart). Although this follows trends observed through HBI assessment, it additionally groups similar communities by reach and season. The analysis also identifies 11 groups that are characterized by 7 indicator species (Table 4, and numbers on the Figure 4 dendrogram). Samples comprising the highest, most general, grouping level that was associated with indicator species was titled 'Upper and Middle Watershed' (Figure 4, Group 1; Table 4). This grouping was associated with taxa that were regularly distributed through most samples and therefore ubiquitous throughout the watershed. The lowest level, and most highly confined, group was WA, titled the 'lowest site – WA' (Figure 4, Group 11; Table 4). The HBI for WA was higher than any other Walker River reach, indicating this is the most tolerant community and this reach may be the most degraded environment (see Figure 2).

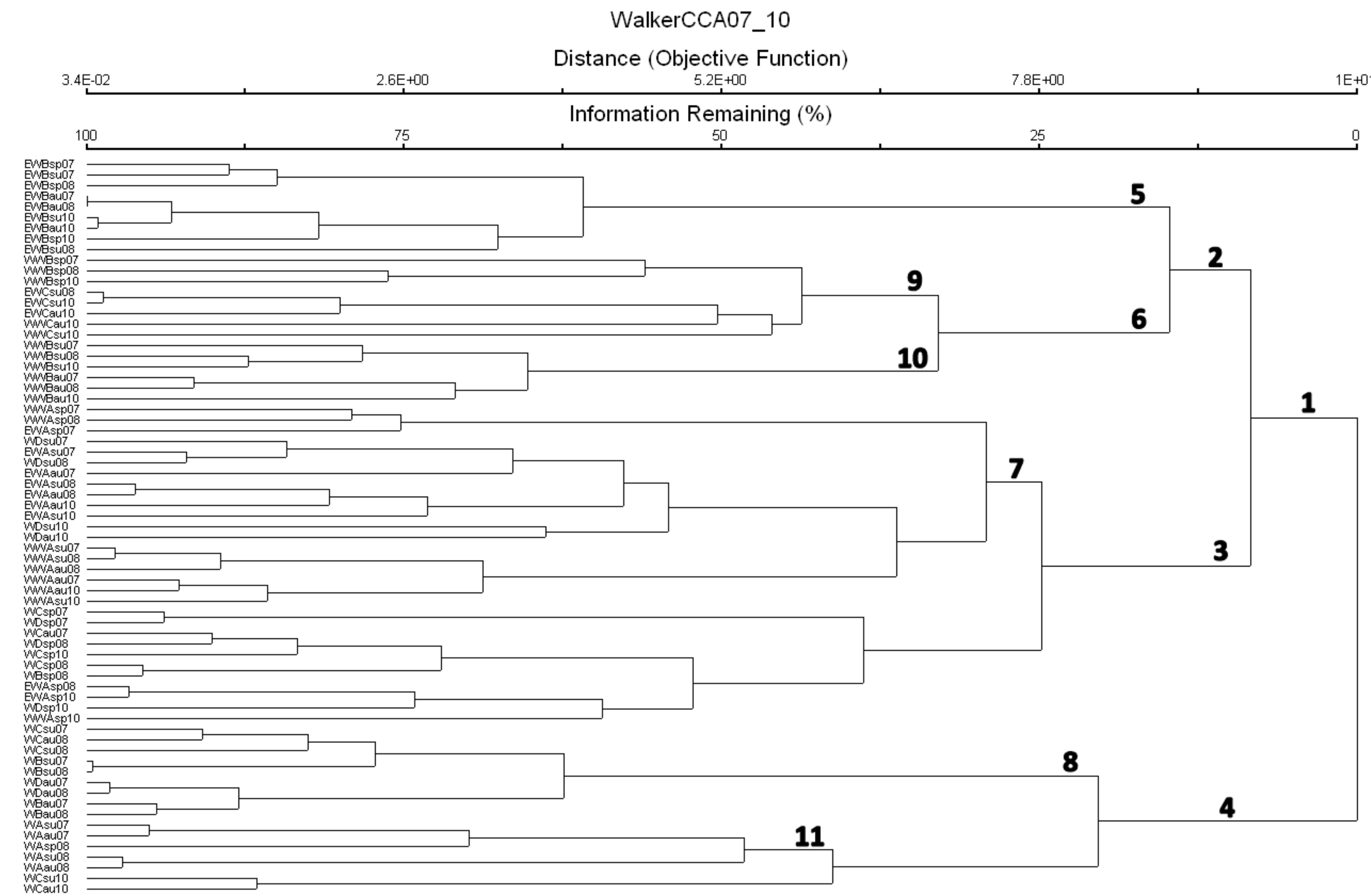

Figure 4. Bray-Curtis cluster analysis dendrogram of Walker River BMI benthic samples. Numbers in bold designate indicator species assemblages described in Table 4.

Table 4. Indicator species assemblages sorted by group based on the Bray-Curtis dendrogram (Figure 4). Peak IV indices for taxa in each group are marked with a '*'. Tolerance values, functional feeding groups, and behavior type are from Ode (2003).

Sample Group *Taxon*	IV Index	Tolerance Index	Functional Feeding Group	Behavior
1. Upper and Middle Watershed				
Baetis tricaudatus	68.8*	5	COLLECTER-GRAZER	SWIMMER
Hydropsyche*	50.8*	4	COLLECTER-FILTERER	CLINGER
Cricotopus/Orthocladius	66.0*	7	COLLECTER-GRAZER	CLINGER
Thienemanniella	60.0*	6	COLLECTER-GRAZER	SPRAWLER
Sperchon	71.2*	8	PREDATOR	CLINGER
2. Upper Watershed				
Optioservus quadrimaculatus	84.5*	4	SCRAPER	CLINGER
Rheocricotopus	62.1	6	COLLECTER-GRAZER	SPRAWLER
Baetis tricaudatus	61.0	5	COLLECTER-GRAZER	SWIMMER
3. Middle Watershed				
Rheotanytarsus	54.8*	6	COLLECTER-FILTERER	CLINGER
Thienemanniella	56.9	6	COLLECTER-GRAZER	SPRAWLER
4. Lower River				
Paracloeodes	56.1	4	COLLECTER-GRAZER	SWIMMER
Tanytarsus	51.1*	6	COLLECTER-FILTERER	CLNGER
Cricotopus (Bicinctus)	64.5*	8	COLLECTER-GRAZER	CLINGER
Ostracoda	68.4*	8	COLLECTER-GRAZER	SPRAWLER
5. East Walker B (all seasons)				
Rheocricotopus	75.2*	6	COLLECTER-GRAZER	SPRAWLER
Tvtenia	52.7*	5	COLLECTER-GRAZER	SPRAWLER
Optioservus quadrimaculatus	62.6	4	SCRAPER	CLINGER
Baetis tricaudatus	54.2	5	COLLECTER-GRAZER	SWIMMER
6. West Walker B and Montane Headwaters				
Ameletus	80.5*	0	COLLECTER-GRAZER	SWMMER
Attenella delantala	57.1*	2	COLLECTER-GRAZER	CLINGER
Epeorus	60.7	0	SCRAPER	CLINGER
Rithrogena	71.4*	0	SCRAPER	CLINGER
Paraleptophlebia	71.4	4	COLLECTER-GRAZER	SWIMMER
Pagastia	52.8*	1	COLLECTER-GRAZER	SPRAWLER
7. Confluence Region				
Acentrella	56.8	4	COLLECTER-GRAZER	SWIMMER
Camelobaetidius	50.7	4	COLLECTER-GRAZER	SWIMMER
8. Valley sites				
Paracloeodes	71.5*	4	COLLECTER-GRAZER	SWMMER
9. Headwaters and WWB Springtime				
Epeorus	74.4*	0	SCRAPER	CLINGER
10. WWB Summer and Autumn				
Sublettea	67.0*	0	COLLECTER-GRAZER	SWIMMER
Ameletus	55.3	0	COLLECTER-GRAZER	SWIMMER
Pagastia	51.0	1	COLLECTER-GRAZER	SPRAWLER
11. Lowest Site - WA				
Paratanytarsus	57.6*	6	COLLECTER-GRAZER	SPRAWLER

The primary split in samples was between the upper and middle watershed and the three lowest reaches, implying a sharp gradient of community and environmental change from the East and West Forks to the main stem Walker River. Secondary divisions indicate significant community and environmental differences between the East Walker River below Bridgeport Reservoir (EWB) and the West Walker site at a similar elevation (WWB). This West Walker site grouped relatively closely with headwater sites (EWC and WWC) on both the East and West Walker forks, which is consistent with HBI assessment that indicates these are reference sites. The paucity of anthropogenic influences on upper West Walker sites (WWB, WWC) and the upper most East Walker site (EWC) suggests that these communities may closely represent 'reference' conditions for the river at these elevations. The similarity in elevation, water temperature, substrate composition, and discharge for EWB and WWB under reference conditions suggests that BMI communities would be similar in these reaches without existing anthropogenic influences.

Samples taken from EWA, WWA, and upper Mason Valley (WC, WD) formed a major group characterized by fewer indicator species than the upstream groups. Community similarities in this 'middle watershed' group appeared to have less spatial and temporal predictability than either upstream or downstream communities. In multiple cases major groupings contained sub-groupings with a unique, or partially unique, set of indicators. (Figure 4, Table 4). An 'anomoly' for reach WD is shown for the summer and autumn of 2010. All 2007 and 2008 WD samples cluster with WC and WB (other downstream reaches in Mason Valley). Summer and autumn WD samples during 2010 differed from this pattern, and were associated with EWA and WWA, which are upstream, in cooler reaches of river. This upstream shift in BMI community characteristics may be attributed to cooler water temperatures and greater discharge in 2010 compared to conditions during the drought of 2007 and 2008.

Segregation of WA in its own group is consistent with HBI assessment indicating this is reach of river is highly degraded. Additionally, this is the only reach occupied by *Paratanytarsus* sp., which is tolerant of harsh conditions.

Benthic Macroinvertebrate Biomass and Secondary Production

A total of 907 animals belonging to 37 taxa were analyzed to estimate secondary production. Sites EWB and WD were not sampled during fall. The number of species at sites WWB, EWB and WWA increased in summer and fall compared to spring, however decreased steadily from spring to fall at downstream sites WD and WC (Figure 5A). Estimated BMI density was highest at sites EWB and WWB (433 and 565 animals m^{-2}, respectively) throughout the sampling and lowest at downstream sites WD and WC (48 and 187 animals per m^{-2}, respectively) (Figure 5 B). Total BMI biomass at each site was highest in spring and decreased during summer and fall (Figure 5 C).

Total BMI biomass was also significantly positively related ($r^2 = 0.9$) to species richness (Figure 6), confirming that maintaining high species diversity is important to maintain biomass available to support Walker River fish populations.

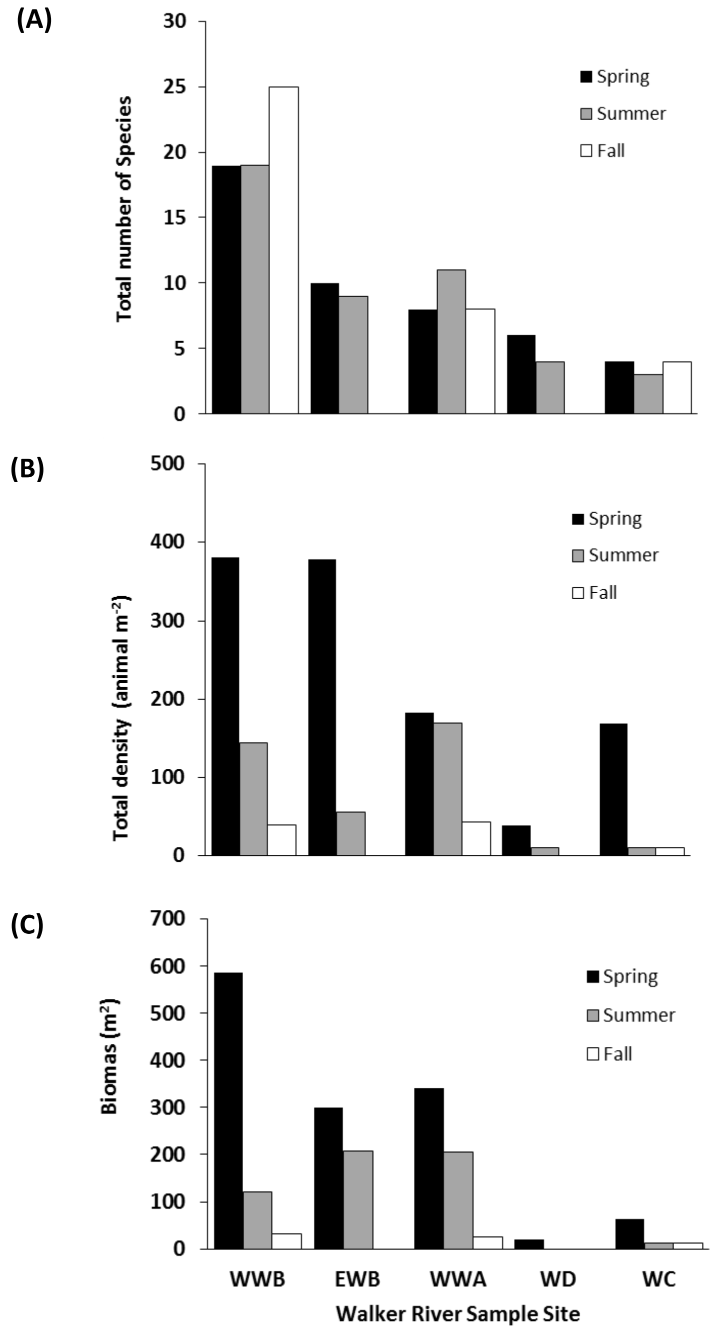

Figure 5. Total number of species (A), density (B), and BMI biomass (C) in spring, summer, and fall for five Walker River sample reaches. Reach codes as shown in Table 1.

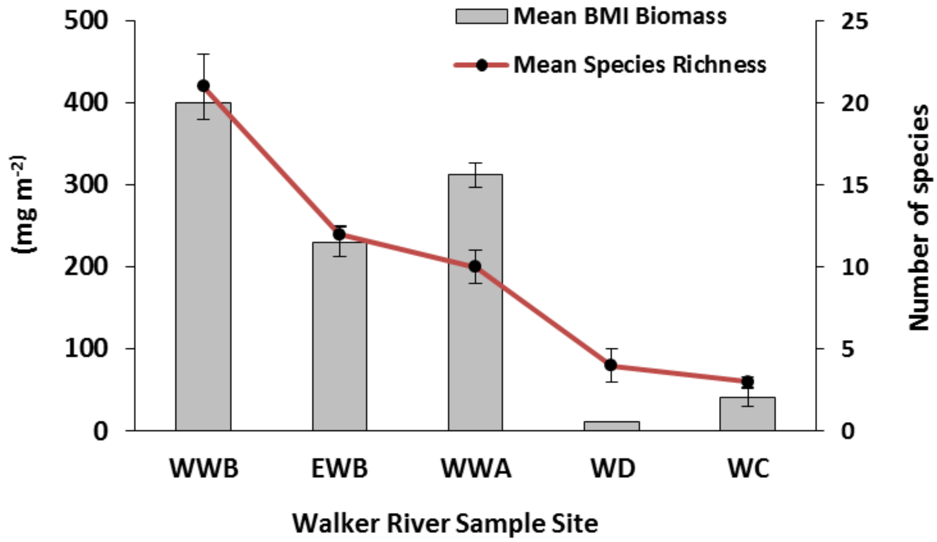

Figure 6. Mean (± 1 standard error) BMI biomass and associated mean species richness for five Walker River reaches. Reach codes as shown in Table 1. Mean biomass and mean species richness include all BMIs collected from April 2010 to Sept. 2010).

Consistent with many other studies (e.g., Culp et al. 1983, Erman and Erman 1984, Kaller and Hartman 2004), substrate size was important to BMI species richness, density, and biomass during the spring and summer of 2010 (Figure 7). Species richness, density and total biomass were also positively associated with substrate size in spring (Fig. 7 A, C, D). These trends were less clear in summer, particularly for density and biomass that seemed to be less affected by substrate size (Fig.7 D, F). Maybe other parameters, such as stream temperature, food quality and quantity might have stronger effects on BMI distribution during summer months.

Only a few taxa were common to all samples. The BMI fauna was dominated by the genera *Baetis*, *Ephemerella*, *Isoperla*, *Rithrogena*, *Serratella*, *Ameletus*, and *Heptagenia*, which combined to constitute 68 percent of the total biomass. The remaining 30 taxa were rare and occurred irregularly during the investigation. Because *Baetis* sp. accounted for about one-third of total biomass in Walker River, secondary production focused on this species only and at sites WWB and EWB which differ in water quality and substrate size.

The annual production was twice as high at site EWB (1.3 g m^{-2} yr^{-1}) compared to site WWB (0.7 g m^{-2} yr^{-1}) (Table 5). These values are lower than those of 2.07 g m^{-2} yr^{-1} estimated by Henneberry (2009) for Walker River *Baetis tricaudatus* populations. The annual P/B ratio was also higher at site EWB (6.46) compared to WWB (5.4). Higher levels of nitrogen and phosphorus at site EWB likely increased the quality and quantity of periphyton, an important food source for the grazer *Baetis* spp., which may have contributed to higher annual production rates in this reach.

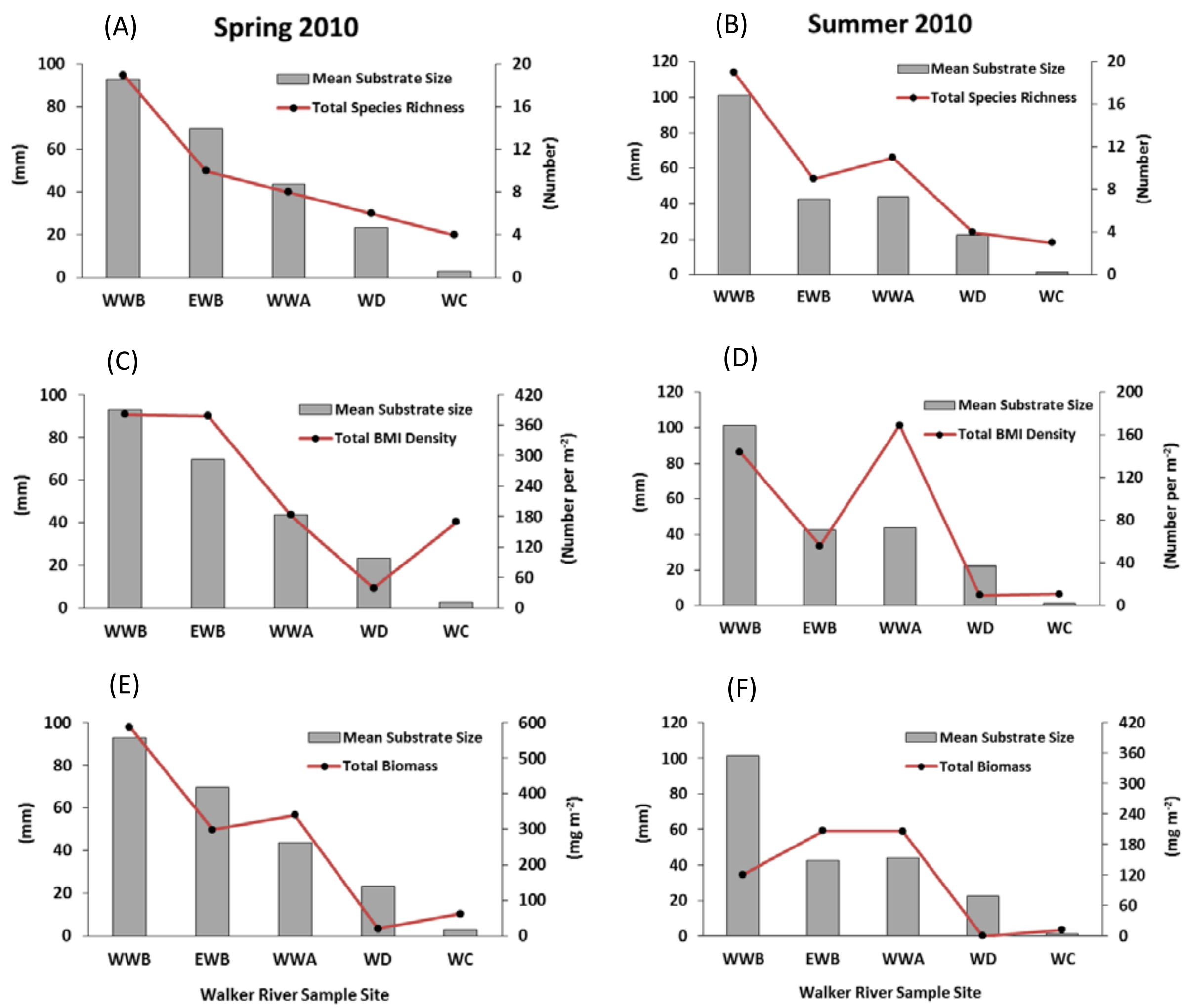

Figure 7. Relationships between mean substrate size (± 1 standard error) and species richness (A and B), BMI density (C and D), and biomass (E and F) for five Walker River reaches during the spring and summer of 2010. Reach codes as shown in Table 1.

Table 5. Annual biomass, cohort production, annual production, and annual average standing production/biomass ratio (P/B) for *Baetis* sp. populations sampled from April 2010 to September 2010 at two Walker River sites.

	Walker River Sample site	
	WWB	EWB
Annual Biomass (B) (g m-2)	0.13	0.21
Cohort Production	0.29	0.55
Annual Production (P) (g m-2)	0.7	1.3
Annual P/B Ratio	5.4	6.46

Baetis sp. biomass was also affected by water temperature (Figure 8). Its biomass was highest and increased at four sites where it was studied during the spring before rapidly decreasing to very low levels (< 20 mg m^{-2}) during early summer and fall. Rapid decreases were observed when water temperature exceeded approximately 12oC at each site.

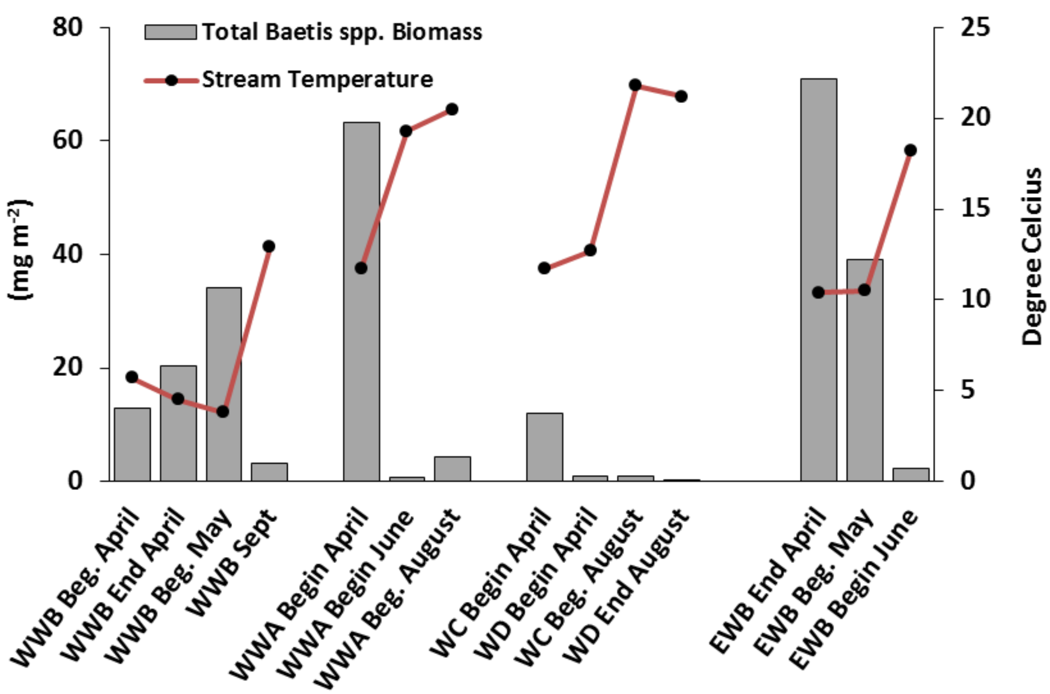

Figure 8. Total *Baetis* sp. biomass for five sites in Walker River during 2010. Samples from reaches WC and WD are combined because these sites were not sampled during autumn. Reach codes as shown in Table 1.

DISCUSSION

Watershed analysis and monitoring are considered essential components of the watershed restoration process. Watershed analysis serves the primary purpose of identifying opportunities and constraints prior to a restoration project so that the project can be planned for optimum impact and cost-efficiency (Kershner 1997). Monitoring serves to measure restoration effectiveness over time by comparing project outcomes with project goals and provide feedback for adaptive management (Downs and Kondolf 2002). Both of these components of the restoration process are often overlooked by restoration practitioners for the sake of cost savings, expediency, or perceived lack of importance (Palmer et al. 2007, Bernhardt 2005, Bash and Ryan 2002). As a result, restoration projects are often planned and evaluated based on subjective, often aesthetic, measures of ecological improvement (Palmer et al. 2007, Kondolf et al. 2007). In cases where watershed assessments are conducted and monitoring is implemented, deficiencies of baseline data or scientific understanding can prove challenging to overcome, especially in watersheds that have not been well studied (Follstad Shah et al. 2007, Kondolf and Micheli 1995).

The initial watershed analysis, the establishment of a baseline data set, and the implementation of monitoring are all made more complex by the dynamic nature of aquatic communities. The cumulative effects of the annual hydrograph structure aquatic communities both spatially and temporally (Lytle and Poff 2004, Strange et al. 1999). Temperature has been shown to have a very significant effect on the structure of benthic communities and generally functions as a longitudinal gradient of increased thermal load in mountainous watersheds of western North America (Boyle and Strand 2003, Hawkins et al. 1997). Finally, increased loads of nutrients and other pollutants can lead to sharp changes in benthic community structure often associated with land use (Cuffney et al. 2000). Furthermore, all of these factors may interact to form more complex gradients of environmental conditions and community structure. Abiotic factors such as flow, temperature, and water chemistry can be seen as a complex set of filters that determine the benthic community at a given location (Poff 1997). Changes to these abiotic 'filters' over space and time may lead to an expansion, contraction, or shift in the community.

The river continuum concept (Vannote et al. 1980) models watersheds as a longitudinal gradient of communities, with a different composition of functional feeding groups in the upper, middle, and lower reaches of a watershed. Temporal changes in flow and water temperature can accelerate, delay, or inhibit the seasonal life cycles of aquatic organisms (Poff et al. 1997, Bunn and Arthington 2002). Anthropogenic changes to flow, temperature, or water chemistry may lead to a longitudinal shift in the community gradient (Voelz and Ward 1990). Understanding and predicting community shifts at the watershed level can be extremely valuable for optimizing flow restoration. Monitoring these shifts over time can lead to valuable insights and inform an adaptive management program. These objectives are particularly valuable in the context of the hydrologic restoration goals of the Walker Basin Program.

Benthic macroinvertebrate community composition is often used as a measure of anthropogenic disturbance in watersheds (Karr 1999), and likewise an important measure of restoration priorities and successes (Poff et al. 2010, Gore et al. 2001). Reference data sets can be used to generate biotic indices to measure present and future conditions (Karr 1981). Benthic macroinvertebrate indices were developed by Tetra Tech, Inc. (2007) for the Walker River, and the nearby Truckee and Carson rivers, as a group. These three rivers are the largest rivers in the western Great Basin and are representative of lotic ecosystems in the region. These methods require the comparison of some component of the community (the index) at the site of interest to the same community component 'pristine' or unimpaired baseline sites designated as 'reference sites' (Reynoldson et al. 1997). This comparison involves two potentially inaccurate assumptions: 1) the baseline site is 'pristine' or the relative degree of disturbance can be accurately assessed so as to function as a precise benchmark by which to measure disturbance at other sites and 2) the component of the community that makes up the index measurably responds to the to the specific impairment or disturbance being addressed.

Biotic indices measure community metrics against a baseline defined by the 'reference condition.' In many ecosystems of the world there are no truly pristine sites, so the reference sites selected are therefore limited to the least disturbed of available sites based on surveys of attributes related to disturbance (Stoddard et al. 2006). Tetra Tech (2007) found that, though the upper (montane) reaches of western Great Basin watersheds contained many sites that were mostly pristine, the lower reaches of these watersheds contained no sites that were free of anthropogenic disturbance or ecological impairment. The synergistic effects of extensive agricultural development and water delivery infrastructure have not missed any aquatic habitats in this arid region. For example, even sites that lie within the relatively undisturbed confines of wildlife refuges or other public lands are inherently affected by hydrologic alteration and pollution from upstream.

Tetra Tech (2007) concluded that existing biotic indices based largely on Hilsinhoff tolerance values (Hisenhoff 1988) and EPT (Ephemeroptera, Plecoptera, Trichoptera) diversity would not accurately describe river health for lower watershed as they would for upper watersheds in the three watersheds studied. The difficulty of establishing accurate tolerance values is a common problem in arid, mountainous, and poorly studied regions of western North America (Blinn and Ruiter 2006). An ideal biotic index to optimize restoration in the Walker Basin would need to accurately measure changes in anthropogenic factors structuring benthic communities from the top of the watershed to the bottom and be sensitive to the effects of hydrograph and temperature as well as the effects of pollution. Existing biotic indices do not function in such a comprehensive manner in the Walker River watershed.

In watersheds that have not been well studied, such as the Walker River and other watersheds of the western Great Basin, a greater understanding of aquatic communities and ecological gradients is needed to effectively assess biotic integrity and river health (Kennedy et al. 2000). To more accurately inform restoration design and assessment, we analyzed Walker basin BMI communities, the river environment, and their seasonal and inter-annual shifts using HBI, ISA, and CCA.

The HBI increased along a gradient from upstream to downstream, showing that environmental harshness increases along elevational and increasing anthropogenic use gradients. This tolerance gradient was associated with increasing anthropogenic disturbance downstream, but may also have been influenced by a covariate trend in elevation and water temperature. Sites WWB, WWC, and EWC were minimally influenced by human activities. Similarities between their HBIs and their occurrence at similar elevations in different sub-drainages suggest these sites can be considered as 'reference' for the East and West Forks at the base of the Sierra Nevada. Knowledge of the environmental conditions prior to the influences of diversion and agriculture in lower reaches of river indicate that this information provides little utility to understanding community-environment relationships in the context of reference conditions (e.g., Poff 1997, Ciesielka and Bailey 2007).

The CCA indicated that BMI communities are most influenced generally by geomorphic factors (i.e., wetted width and substrate), elevation and temperature related factors, and nutrients. This suggests that factors influencing nutrients, water temperature, and substrate may be the most important parameters to be considered and managed for river restoration.

Several associations shown by ISA, and clarified by HBI and CCA, are important to set restoration goals and design restoration programs. First, restoration must be tailored to address different environmental characteristics that occur from the base of the Sierra Nevada to Walker Lake. The ISA suggests there are four distinct environments, upper watershed (EWC, WWC, WWB), middle watershed (EWA, WWA, WD, and maybe WC), lower Mason Valley (WB), and lower river (WA). Results from the three analyses indicate that distinctive goals may be appropriate for each of these areas.

The paucity of anthropogenic influences on upper West Walker sites (WWB, WWC) and the upper most East Walker site (EWC) suggests that these communities may closely represent 'reference' conditions for the river at these elevations. The similarity in elevation, water temperature, substrate composition, and discharge for EWB and WWB under reference conditions suggests that BMI communities would be similar in these reaches without existing anthropogenic influences. This is also suggested by CCA which separates EWB from reaches due to elevated nutrients that distinguishes the environment in this reach from others. It appears that little restoration is needed for WWB, WWC, and EWC, and that resolving nutrient levels is an appropriate first step to restoring EWB.

Another association involves reach WD, which was the highest reach sampled in the main stem Walker River. All 2007 and 2008 samples in this reach cluster with WC and WB (other downstream reaches in Mason Valley). Summer and autumn WD samples during 2010 differed from this pattern, and were associated with EWA and WWA, which are upstream, in cooler reaches of river. This upstream shift in BMI community characteristics may be attributed to cooler water temperatures and greater discharge in 2010 compared to conditions during the drought of 2007 and 2008. This shift also suggests that BMI communities that characterize EWA and WWA may extend downstream into Mason Valley under increased discharge and decreased temperature conditions, and that reference conditions for upper Mason Valley may resemble conditions in EWA and WWA. It is reasonable to assume restoration of upper Mason Valley reaches may occur when creating temperature and discharge conditions in this area allow extension of the less tolerant EWA and WWA communities into the upper reaches of the main stem Walker River (e.g., WD and WC).

The absence of information describing reference conditions through Mason Valley, active agricultural diversion and accretion in this reach, and restricted spatial and temporal variability in environments and BMIs during this study limits the utility of this study to address restoration issues for this portion of river. This portion of river may respond to lower water temperatures and greater discharge, but BMI richness and biomass may be limited by the sand and small gravel substrates that characterize this reach (see Adams in Collopy and Thomas 2010).

Downstream-most portions of the river (e.g., WA) are highly degraded, mostly by reduced discharge. This is the only reach occupied by *Paratanytarsus* sp., which is tolerant of harsh conditions. Improving conditions in this reach so that it is no longer occupied by *Paratanytarsus* sp. (or other highly tolerant species) would indicate an improvement of river habitat.

The influence of river environment that is indicated by multivariate analyses (e.g., CCA and ISA) is confirmed by more definitive assessments of specific environmental parameters. The inverse association of BMI species richness, density, and biomass with substrate size suggests that food may be limited for higher trophic levels (i.e. fish) where substrates are small. This is particularly important through Mason Valley down to Walker Lake where substrates are naturally small due to geomorphology and the low gradient through this portion of river. This characteristic suggests that BMI productivity (i.e. secondary production) in this reach of river cannot achieve levels observed in the East Walker and West Walker where substrates are large. It also suggests that food resources available to fish are greater in the East Walker and West Walker than in lower reaches of river.

Secondary production studies that focused on *Baetis* sp. found that its biomass in the river is greatest during early spring, and it rapidly decreases by early June. *Baetis* sp. biomass was also affected by temporal variability in water temperature. Additional work is needed to more definitively quantify temperatures that negatively affect its biomass, but preliminary assessment suggests that this occurs when water temperature exceeds 12^{o}C.

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