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Understanding effects of changes in land use, environmental parameters, habitat characteristics on the Great Basin aquatic invertebrates using ecological stoichiometric theory

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UNDERSTANDING EFFECTS OF CHANGES IN LAND USE, ENVIRONMENTAL PARAMETERS, HABITAT CHARACTERISTICS ON THE GREAT BASIN AQUATIC INVERTEBRATES USING ECOLOGICAL STOICHIOMETRIC THEORY

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ABSTRACT

Understanding effects of changes in land use, environmental parameters, habitat characteristics on the great basin aquatic invertebrates using ecological stoichiometric theory

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Many freshwater ecosystems in the Great Basin have undergone dramatic alteration over the past decades due to groundwater withdrawal, water diversion and changes in land use. These changes have affected benthic food web dynamics by altering the availability of chemical key elements for primary and secondary producers, by loss of biodiversity and extinction of endemic species. However, only few studies are available that addresses the link between changes in land use, habitat characteristics and its effects on benthic macroinvertebrates (BMI) communities comprehensively and little attention has been given to integrating physiochemical aspects to link ecosystem functions.

This dissertation analyzes the link between BMI communities and their habitat characteristics in the Walker River and in diverse spring ecosystems in the Great Basin by using ecological stoichiometry and secondary production assessment as tools and provides a knowledge base that can be used in stream and spring protection and restoration, respectively.

The dissertation includes three separate studies that are organized into three chapters that are being prepared for peer reviewed publication. In the first study, multiple regression analysis followed by corrected Akaike's Information Criterion (AICc) was used to determine predictor variable(s) that best explains the elemental composition of basal food resources (seston and periphyton) and BMI along an elevation gradient and land use type in the Walker River in California and Nevada. The elemental composition of basal food resources are best explained by land use and associated differences in soluble reactive phosphorus (SRP),dissolved organic carbon (DOC), and stream water nitrogen (N): phosphorus (P) ratios. In contrast, BMI elemental stoichiometry was correlated to taxonomic identity and body mass. Therefore, both parameters should always be taken into account when addressing land use effects on resource-consumer stoichiometry. Consumer-resource elemental imbalances in this study were less pronounced than those reported from the nutrient-poor streams. However, high spatial and temporal variability in food source elemental composition obscured clear spatial pattern in elemental imbalances between nutrient-poor upstream sites and nutrient-rich downstream sites.

Results from this study suggest that applying ecological stoichiometry is a useful tool to better understand the elemental dynamics of food components particularly in

Great Basin watersheds with highly variable physiochemical conditions that such as Walker River.

The second project analyzed the link between the ecological health of BMI communities and habitat characteristics along the Walker River. Biotic indicesindicated a shift in BMI communities towards species-poor assemblages with few dominant taxa from upstream to downstream parts of Walker River.Further, the Hilsenhoff Biotic Index (HIB) indicated an increase in the dominance of pollutant-tolerant taxa at downstream parts of Walker River. These shifts in the BMI community compositionwere related to spatial changes in substrate size, stream width, stream temperature, SRP, and Total Suspended Solids (TSS).

Further, secondary production of *Baetis* mayflies, one of the most common genera in Walker River, was estimated between two sites differing in water quality to assess effects of nutrient enrichment on *Baetis* density, biomass and secondary production. Although mean individual body mass of *Baetis* was lower at the nutrient enriched site, secondary production was higher most likely due to the combination of higher growth rates and higher densities.

Based on these results I recommend that factors influencing nutrients, discharge, and stream temperature are the most important parameter to consider Walker River restoration.Further, the results from this study can be used to assess the success of stream restoration by documenting changes in BMI communities and secondary production.

In the third study, spring-dwelling snails and their potential food source were collected from twenty-three springs from the eastern part of the Great Basin to provide a basic understanding about the link of the snail’s elemental composition to taxonomy, basal food resources and habitat characteristics. The results showed that body% phosphorus (P)of snails was highly variable among the four major snail families whereas body% nitrogen (N) and % carbon (C) varied less. Differences in the body elemental composition among the same species collected from multiple springs indicate that aquatic snails can deviate from strict homeostasis. The body %P content in snails belonging to *Pyrgulopsis*collected from warm springs (water temperature $\geq$ 20ºC)was significantly lower compared to those collected from cold springs.Further, elemental imbalances between snails and there potential food sources were significantly higher in warm springs compared to cold springs.

These results indicating that water temperature is an important factor that constraints food web dynamics in long-term stable ecosystems, such as springs. Basic understandingabout food web dynamics in Great Basin springs is not only important to determinefurtherconsequenceson the nutrient cycling in ecosystems with strong temperature gradients. It can also be used to predict consequences of human alterations on the food web dynamic in these long-term stable ecosystems.

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CHAPTER 1

INTRODUCTION

Aquatic and associated riparian ecosystems represent only 0.5-1.0% of the land surface in the eleven western most states of the continental United States (GAO 1988) and are characterized by high biological diversity (Chambers and Miller 2004; Sada and Vineyard 2002). These ecosystems are facing degradation in water quality and associated decline in biodiversity. Most of the aquatic ecosystems in the Great Basin have been altered from undisturbed conditions. Degradation has been attributed to excessive surface and groundwater use due to expanding urbanization and agriculture, altered discharge due to construction of dams and diversions, excessive use of non-native ungulates, and invasion of non-native species (Sada et al. 1992; Fleischner 1994, Rood et al. 2003). One of the greatest impacts on water quality of many Great Basin aquatic ecosystems originated from agricultural practices (UDWQ, 2004; Sada 2008; Torregrosa and Devoe, 2008). These activities have already changed cycles of water, sediments, and elements (Falkowski et al., 2001; Tilman et al., 2001; Foley et al., 2005). Water quality has been altered by point and non-point source pollutants include nutrients, metals, sediments, and elevated water temperatures (Sada, 2008). The impact of such changes in stream ecosystems has been profound. There are very few studies that deal with such changes on food web components, such as primary (benthic algae, periphyton) and secondary (benthic macroinvertebrates) producers in the Great Basin watersheds. Existing studies are narrow and only focus on specific aspect of changes in primary or secondary producer community composition or biodiversity (Hampton et al., 2002; Davis et al. 2010; Jannush et al., 2011). There is no study available for Great Basin watersheds that link trophic levels by integrating the distribution of key nutrient elements, such as carbon (C), nitrogen(N) and phosphorus (P) within food webs that provide comprehensive understanding of the relation by focusing in interaction between the primary and secondary consumers.

Ecological stoichiometry is one of the few ecological concepts has been applied quantitatively to study the balance of energy and chemical elements across many levels of biological organization and ecological interactions from individual cells up to the biosphere (Sterner and Elser, 2002).The rationale of incorporating ecological stoichiometry into research on aquatic ecosystems is that links traditional disciplinary boundaries between environmental chemistry, biochemistry, ecology and evolutionary biology by using chemical elements as natural currencies (McIntyre and Flecker, 2010). Fluxes and pools of these elements can be quantified at any spatial or ecological scale (McIntyre and Flecker, 2010) and the relative availability of elements determines which one mostly constraints ecological processes.

1.1 Walker River

In ecological studies, particularly the distribution of C, N and P in biomass are of interest, because C is the energy source where N and P can limit autotrophic production and are also likely important for heterotrophs (Andersen et al., 2004). The effects of these elements on ecological and trophic interactions in streams have been examined by using ecological stoichiometric theories (Sterner and Elser, 2002). Commonly, N and P are limiting nutrients for autotrophic production and also likely affect heterotrophic organisms. Because consumers are richer in N and P than their food, the imbalance in elemental composition can affect consumer performance, such as their growth, reproduction, abundance, and nutrient cycling (Cross et al., 2003; Frost et al., 2002; Stelzer and Lamberti 2001; Evans-White et al., 2005). Numerous studies have contributed to the understanding of nutrient limitation (Sterner and Elser, 2002), trophic interactions (Elser et al., 1998; Sterner et al., 1998), nutrient cycling (Elser and Urabe, 1999; Vanni, 2002), and population dynamics (Stelzer and Lamberti, 2001; Andersen et al., 2004; Moe et al., 2005). Although, it has been shown that climate change and land use change can affect the abundance and distribution of key elements in streams (Carpenter et al., 1998; Cross et al., 2003), effects on the elemental composition in higher trophic levels are inconclusive. For example, Bowman et al. (2005) found little variation in consumer elemental composition between P enriched sites and P depleted sites. However, due to changes in the elemental composition of their food source at P enriched sites, elemental imbalances were relaxed and the consumer N:P recycling ratio was significantly different between the two sites. In contrast, Small and Pringle (2010) reported higher P contents in different BMI consumer assemblages when they were exposed to high P loads over a long time period. Similarly, in an experimentally enriched detritus based stream with N and P, Cross et al. (2003) reported significant increases in the nutrient content of the food source and in some BMI taxa. In a study among streams within in an urban catchment, Tsoi et al., (2011) did not find a relation between land use, nutrient concentrations and the C, N, and P content in both producer and consumer. However the spatial and temporal variability in BMI body C, N, and P content was related to the variability of nutrients attributed to anthropogenic affected streams. It seems that the exposure time and the amount of nutrient inputs play a role in affecting the elemental composition of stream BMI. Other studies have assessed the effect of water pollution and withdrawal on the alteration of community composition of stream biota (Ometo et al., 2000; Azrina et al., 2006). Excessive nutrient inputs together with excessive surface and groundwater withdrawals have led to the loss and extinction of sensitive and endemic species and the increase of pollution tolerant and invasive species (e.g. Sada et al., 1992, Delong and Brusven, 1998; Harding et al., 1999; Bustos-Baez and Frid, 2003). Although progress has been made in using stoichiometric models to understand processes that link environmental factors to key nutrients and biota in stream ecosystems, further descriptive information is needed and should be expanded to a broader variety of stream ecosystems. Particularly streams in semi-arid and arid regions are understudied (Grimm and Fisher 1986; Grimm, 1988; Parker, 1989) and only few studies have addressed Great Basin streams (Kennedy et al. 2000; Sada, et al. 2005; Myers and Resh, 2002). The Walker River, Nevada, is representative for a Great Basin stream, characterized by its high variability in longitudinal stream gradients, bed rock material, water temperature and clarity, human impacts, and surrounding land use. Agricultural activities along the middle and lower reaches of Walker River have been identified as the major contributors which lead to degradation in water quality and quantity along its flow path. Its downstream reaches have been extensively used for irrigation and agriculture since 1860 (Sharpe,2009; Hayveart et al., 2009) and consequently the annual flow of the Walker River has dropped from 11.3 m^3/s by the end of the 19th century to almost zero in the 1980’s. Lower reaches of the Walker have been altered by reduced flow and increased agricultural runoff that has added nutrients, such as

P, N, and C. This has caused a strong nutrient gradient, ranging from 4.5-40.5 µg/L for ammonia-nitrogen (NH_3-N) and from 8-102 µg/lfor total phosphorus (TP) at undisturbed and heavily influences sites, respectively (Sharpe2009). Although studies regarding community composition and abundance of both primary producer (algae, periphyton) and BMI have been conducted along the nutrient and elevation gradient, no information is available on the elemental composition for the Walker River. This study about elemental composition of both BMI and their food source will examine broader ecological processes than can be determined from BMI community studies only and will also increase the accuracy in biological integrity assessments along the Walker River.

1.2 Nutrient Driven Secondary Production and Population Change of Benthic Macroinvertebrates along Walker River: Is Nutrient Pollution Helping?

The quality and amount of productivity 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). In streams, BMI dominate the secondary production and play an essential role in transferring material and energy through benthic food webs (Huryn and Wallace, 2000). The production of a certain 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/area) and production is the accrual of biomass of an organism or a population over a certain time period per unit area (mass·area^{-1}·time^{-1}). The Production/B ratio provides a comparison of growth rates of species between 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 an organism's life history patterns strongly depend 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 follow a strong longitudinal gradient caused by changes in stream size, resource availability, and temperature (Vannote et al., 1980). However, anthropogenic impacts can alter this longitudinal relationship. In a comprehensive literature study including 200 streams, Finlay (2011) demonstrated that food quality (i.e. P availability) has the strongest control over secondary production. Because P and dissolved inorganic nitrogen (DIN) availability increased in anthropogenic altered watersheds, autotrophic and heterotrophic organisms were released from nutrient limitation. For example, Cross et al. (2006) elevated the nitrogen and phosphorus concentration in a detritus based headwater stream for two years and observed that enrichment had increased secondary production of higher metazoan significantly by approximately 22% compared to a reference stream. This was attributed to the increased quality of detritus in the nutrient enriched stream as shown in the significant relationship between secondary production and magnitude of nutrient enrichment in streams. Along a Great Plains stream affected by urban and agricultural activities, Shieh et al. (2002) observed a positive correlation between the degree of pollution by wastewater, urban runoff and agriculture and secondary production, which they attributed to relatively low predation pressure and high nutrient availability.

Alterations in the quantity of food source and stream temperature were attributed as important covariate which can affect secondary production (Finlay, 2011). For example, the increase of photosynthetic active radiation by modulations of riparian vegetation was related to changes in primary production and consequently the amount of food available for the secondary consumer (Mulholland et al., 2001). Even small changes in stream temperature due to removal of riparian vegetation can have direct effects on stream BMI in terms of growth, metabolism, reproduction, emergence and distribution of aquatic BMI (Benke and Parsons, 1990; Benke and Jacobi, 1994). Temperature constraints almost all biological activities, such as biochemical reactions, metabolic rates, and rates of biomass production (Brown et al., 2004). Therefore, the rates of secondary production and P/B ratio increase with temperature, attributed to an increase in growth rates, development times and feeding rates. The number of generations per year - referred to as voltinims - also depends on temperature. Clifford (1982) observed that mayflies, commonly univoltin, may switch to a multivoltin life cycle when temperature increased. In a study on mayflies in southeastern Pennsylvania, larvae completed development in 27 days at a temperature of 25°C and 179 days at a temperature of 10°C (Sweeney, 1984).

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. One the other hand, anthropogenic impacts can alter community composition and favor the abundance of taxa tolerant of degraded habitat conditions. These alterations in community structure in turn are expected to offset increased production for higher trophic levels by increasing the amount of unpalatable taxa and consequently reduce the production of 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. Studies on secondary production in streams in semi-arid regions particularly those related to anthropogenic induced alterations are not very frequent (e.g. Jackson and Fisher 1986; Gaines et al., 1992). Recently, only one study has estimated secondary production along the Walker River, Nevada (Henneberry, 2009) using the species *Baetis tricaudatus* using pooled samples collected at various locations. That might be the reason for the relatively low secondary production of 2.07 g/m^2yr^{-1} in the river. The problem of pooling results from different sites along a river is that anthropogenic effects on secondary production (higher food quality due to nutrient inputs) cannot be determined. A comprehensive study including BMI community composition and secondary production is not available for the Walker River. This information however, is essential to assess, which parts of the river are more or less affected, respectively, particularly with regard to the diverse fish populations in the upstream parts of the river (Sada, 2000).

1.3 Great Basin Springs Ecosystems: A Case Study Using Ecological Stoichiometry

Springs have long been recognized as unique ecosystems differing from other aquatic systems by their individual water clarity, extreme ranges in water temperature, physicochemical long-term stability (Odum, 1957; Malanson and Kay, 1980), and complex biotic and trophic interactions (Collins et al., 1976). Particularly, desert springs are scientifically important because they are often the only source of water, because they are often isolated, and because effects of habitat fragmentation after the Pleistocene era on population distribution, population genetics, and species specialization can be observed (Myers and Resh, 2002). Endemism is common in many springs and evolutionary theory predicts that some aquatic organisms may adapt by directional selection to these stable habitats (Taylor, 1985; Williams and Danks, 1991; Erman and Erman, 1995; Ferrington 1995; Williams, 1996; Hershler, 1998; Nekola, 1999; Baldinger et al., 2000; Polhemus and Polhemus, 2002, Zullini et al., 2011). Thus, it can be assumed that spring-dwelling organisms may be different in terms of temperature and pollution tolerance compared to conspecifics in less stable habitats such as lotic or lentic systems. Because temperature influences metabolism, growth rate, and elemental composition in poikilothermic organisms (Atkinson, 1994; Woods et al., 2003) it can be further assumed that spring organisms are stoichiometrically different among springs and among other freshwater systems.Variability in population size and assemblage structure of aquatic life in persistent springs is low compared to other aquatic systems, and springs are often occupied by animals that cannot occupy highly variable environments (van der Kamp, 1995). These characteristics suggest that processes influencing life in springs are trenchantly different than those affecting lotic ecosystems, and that knowledge of lotic system ecology may have little relevance to spring systems. Consequently, bio-assessment indicators that are important to assess lotic system health may be weakly relevant for springs.

It has already been recognized that anthropogenic activities affect springs ecosystems at the global scale (Williams and Williams, 1998; Sket, 1999). This is particularly a problem in the arid southwestern United States. Springs in semi-arid regions are high priority ecosystems, because of their ecological importance isolation from other water bodies, high levels of endemism, and susceptibility to droughts (Shepard, 1993; Thomas et al., 1996; Unmack and Minckley, 2008; Hershey et al., 2010). The most apparent anthropogenic factors influencing desert springs ecosystem are (a) decreasing the groundwater level by excessive water withdrawal and (b) the pollution of groundwater, particularly with phosphorus and nitrate-nitrogen (Scott et al., 2004). Withdrawal of water can reduce the total amount of water available to aquatic biota and can lead to large losses of habitat (Tyedmers and Ward, 2001). Withdrawal of groundwater for agriculture in adjacent areas can completely dry up springs, even if the habitat itself is protected (McDowall, 1984). Water that is withdrawn from those systems is often returned in the form of household wastewater, agricultural runoff, or industrial cooling water, with reduced quality (increased pollutants, changes in nutrient load, etc.) and altered temperature. The Nevada Heritage Program and its Wetlands Priority Conservation Plan (Skudlarek, 2006) identified many of the springs in Nevada as high priority wetlands. During 2007 and 2008, 320 springs were visited to assess their condition and compare current conditions to records compiled during the early 1990s.

These surveys found that 60% of springs are currently degraded by livestock use, 50% by dredging, impoundment, and channelized spring brooks, and 42% by diversion into pipes and tanks (Abele, 2011). Point and non-point source pollution from nutrients, metals, sediment, elevated temperature, and total dissolved solids have degraded water quality in many Great Basin springs. Relationships between disturbance and characteristics of spring-fed biological communities are poorly understood. In 63 southern Nevada springs, Sada et al., (2005) and Fleishman et al., (2006) found that land use, similar to those documented by 2008 and 2009 surveys, affected aquatic and riparian communities by decreasing species richness and altering community structure and biological integrity (Frey, 1977). These findings are similar to disturbances recorded during spring surveys of approximately 1500 Nevada springs in the early 1990's. Many studies have recognized the loss of biological integrity due to anthropogenic impacts on many springs ecosystems, those studies have examined components of ecosystems such as changes of physico-chemical water quality parameters (Galas, 2005), vegetation dynamics (Patten et al., 2008), plant diversity (Nabhan, 2008), plant communities (Cornett, 2008; Meretsky, 2008), and vegetation structure (Spence 2008) or on changes in BMI community composition (Cantonati and Ortler, 1998; Sada and Herbst, 2008). Ecological studies of arid land springs in the western U.S. have lagged behind studies of other aquatic systems, and restoration and management programs are in their infancy (Sada et al., 2001). Most work has focused on biogeography, systematics, taxonomy, and conservation biology of fishes (e.g. Naiman and Soltz, 1981; Williams et al., 1985) and the taxonomy and biogeography of springsnails (e.g., Hershler, 1998; Hershler and Sada, 2002), and a few studies have examined spring vegetation (Fleishman et al., 2006; Patten et al., 2007).

Basic information as well as inventory and mapping data are still lacking and a comprehensive understanding of ecosystem processes in spring ecosystems is still lacking (Stevens and Meretzky, 2008). Ecological work in arid land springs has been limited to select areas and relatively few springs. Moreover, recent studies scarcely examined springs ecosystems stoichiometrically (Elser et al., 2005). Without basic knowledge on the abundance and distribution of key elements, it is very difficult to understand the link between environmental parameters and spring community composition to predict consequences of anthropogenic impacts.

1.4 Motivation and Objectives

Freshwater ecosystems in the southwestern United States are confronted with an increased degradation in water quality that has caused a decrease in biological health and biodiversity in these systems. However, the impacts on relationships between primary producers and secondary consumers are not well studied in especially in the Great Basin watersheds. Ecological stoichiometric tool and measurement of secondary production would greatly help to improve the understanding and assessment of the biological health in freshwater ecosystems in semi-arid areas.

Research Objectives

The three main objectives of the thesis are:

- Characterizing trophic relationships between BMI’s and their potential food source and linking these relationships to land use in a Great Basin watershed by using ecological stoichiometric models

- Linking biological health along Walker River to physical and chemical site characteristics using biodiversity indices and secondary production of BMI
- Understand the effects of habitat characteristics on the elemental composition of aquatic snail species collected from twenty-threespring ecosystems along an elevation and temperature gradient.

1.5 Format

This dissertation is organized in an introduction, three chapters followed by a conclusion and recommendations. Chapter 1 provides background information about effects of anthropogenic impacts on streams and spring ecosystems and how this has altered aquatic biota. The chapter also discusses data gaps and needs for studies. Chapter 2 describes the spatial and temporal variation in elemental composition of basal resources and BMI along a land use gradient in the Walker River. Chapter 3 characterizes the link between biodiversity, secondary production and habitat characteristics along the Walker River. Chapter 4 describes the link between the elemental compositions of aquatic snails to habitat characteristics in spring ecosystems along an elevation gradient. Chapter 2, 3 and 4 will be submitted as manuscripts to appropriate journals.Chapter 5 contains the conclusion and suggested recommendations for future research.

CHAPTER 2

ELEMENTAL STOICHIOMETRY OF BASAL RESOURCES AND BENTHIC MACORINVERTEBRATES ALONG A LAND USE GRADIENT IN A GREAT BASIN WATERSHED

Abstract

Land use and land cover change affects the ecological health of aquatic organisms. Such changes have been explained using ecological stoichiometric theories in temperate and humid ecosystems, but not on aquatic organisms in semi-arid watersheds. Semi-arid streams in the Great Basin are characterized by high gradients in water temperature, discharge and land use. This can result in a high variability of nutrient loading, which likely alters the elemental composition of food web components. In eight sub-watersheds differing in land use, we used multiple regression analysis followed by Akaike's Information Criterion (AIC) to determine which predictor variable(s) best explains the variability in two basal food resources, seston and periphyton and BMIalong Walker River in California and Nevada. We have shown that elemental composition of basal food resources are best explained by land use and associated differences in SRP, DOC, and stream water N:P ratios. In contrast, BMI elemental stoichiometry was rather related to taxonomic identity and body mass. Therefore both parameters should always be taken into account when addressing land use effects on resource-consumer stoichiometry. Food-related differences in some of the BMI taxa support previous studies that consumer can deviate from strict homeostasis. Consumer-resource imbalances were related to feeding mode and were higher for collector-gatherer than for scraper and collector-

filterer. Consumer-resource elemental imbalances in this study were less pronounced than those reported from nutrient-poor streams. However, high spatial and temporal variability in food source elemental composition obscured clear spatial pattern in elemental imbalances between nutrient-poor upstream sites and nutrient-rich downstream sites.

Results from this study suggest that land use can affect the elemental composition of benthic macroinvertebrates by changing the stoichiometry of their food resources and that taxonomy and allometry must be taken into account to better explain spatial and temporal changes in the elemental composition of benthic macroinvertebrates.

2.1 Introduction

Along stream flow paths land use patterns can vary considerably and consequently affect stream ecosystems at multiple scales (Vannote et al., 1980; Townsed et al., 2003). While headwaters of many streams in the Great Basin are occupied by forest, increasing distance from the headwaters is usually correlated with an increase of agricultural and urban areas (Smith, 2000). Influence of land use on physical and chemical water quality parameters has become the central object of stream and river ecology (Wiens 2002; Allan 2004). Human activities and related land use changes have been recognized as primary contributors to physical and chemical changes of water quality parameter in many streams. However, considering land use as a single predictor variable can lead to bias in the interpretation of effects on those variables. Strong seasonal effects on turbidity, ammonium, and SRP have been observed in agricultural impacted streams with higher concentrations during the growing season in summer

(Hoorman et al., 2008). Soulsby et al., (2001) related seasonal changes in water quality in mountain streams due to discharge-related hydrograph changes during spring and summer season.The increase in concentration of organic constituents such as N and P (Harding et al., 1999; Bowes et al., 2003) combined with changes in the natural hydrograph (Walsh et al., 2005), can alter the temporal and spatial availability of nutrients to primary producers (Wold and Hershey, 1999; Sterner and Elser, 2002). The elemental composition of suspended particulate organic matter (hereafter, seston) and periphyton can be controlled by a combination of proximate and ultimate variables (O'Brien and Wher, 2010) such as land use, dissolved nutrient, temperature, turbidity and hydrography. Frost et al. (2009) showed that the C:N, C:P, and N:P ratios of stream seston was best explained by a combination of catchment characteristics and seasonal changes in discharge. Similarly, periphyton C:N, C:P, and N: P ratios in urban streams were best predicted by a combination of dissolved nutrient, such as phosphorus and land use (O'Brien and Wehr, 2010). Because, seston and periphyton are important food sources for collector-gatherer and collector-filterer there is a need to understand the controls on the elemental composition of those food sources. However, information on the extent to which land use and associated water quality parameter affect basal food resources in streams is still scarce for semi-arid watersheds.

Since its application to lotic ecosystems, ecological stoichiometry has greatly contributed to knowledge of stream ecosystem processes by examining the transfer of energy through trophic interactions (Fisher and Likens 1973; Minshall, 1978). Because basal food resources are non-homeostatic with regard to nutrient supply, their elemental composition can vary along longitudinal stream gradients (Sterner and Elser, 2002). In forested headwater sites, BMIs are confronted with low food quality causing strong consumer-resource imbalances (Cross et al., 2007, Sterner and Elser, 2002). However, consumer-resource imbalances can be relaxed due to anthropogenic nutrient enrichment and consequently increased food quality (Bowman et al., 2005). Many studies have investigated combined effects of land use and season on elemental composition of basal food resources and BMI in streams in temperate and humid climates (e.g. Bowman et al., 2005; Cross et al., 2007; Tsoi et al., 2011). Few studies described trophic relations of basal food sources and invertebrate consumers in desert streams (e.g. Gaines et al., 1989; Schade and Fisher, 1997), and even fewer studies have considered relationships between basal food sources and BMIs along longitudinal gradients in semi-arid streams on a stoichiometric basis (e.g. Grimm, 1988; Petersen and Grimm, 1992). Furthermore, studies on the elemental composition of a wide variety of BMI belonging to different taxonomic groups are scarce for these ecosystems. Physical and chemical characteristics of streams in semi-arid watersheds differ widely from those in temperate regions. Highly variable discharge (Velasco et al., 2003), episodic terrestrial-aquatic interaction (Grimm et al. 2004) and to low N:P ratios (Green and Finlay, 2010) due to nitrogen limitation are the key characteristics in many desert streams (Grimm and Fisher, 1986; Grimm, 1988). The regional hydrology of streams within the Great Basin is controlled by the geology and high amount of spatial variability of evaporation and precipitation; however, natural hydrological settings of many streams have been degraded by anthropogenic activities, such as agriculture and urban development (Chambers et al. 2011).

The three objectives of this study were to: (a) examine effects of distances from headwater (DHW, here as a proxy variable for changes in land use along the flow path) and season on physical and chemical water quality parameter, (b) determine predictor variables, which best explain the variation in the elemental composition of basal food resources and BMI, and (c) determine the consumer-resource imbalances along the longitudinal gradient in Walker River. We expected BMI to be less constrained by their food at nutrient-rich downstream reaches compared to those in upstream parts of the river. Finally, by comparing results from this study with those from streams in temperate and humid regions will contribute to determining if region-related stream characteristics can explain the patterns in elemental composition of lower food web components and can, therefore, increase our general understanding in producer-consumer stoichiometry in a wide variety of stream ecosystems.

2.2 Materials and Methods

2.2.1 Site Selection and Data Sampling

Sampling sites were located along Walker River, a first- to forth-order stream located in California and Nevada (Figure2.1). The river is representative of a Great Basin semi-arid stream, characterized by its high variability in longitudinal stream gradients, variability in water temperature and clarity, and with a variety of surrounding land uses. Walker River has a watershed area of 7860 km^2 and flows about 250 km from its headwaters in the Sierra Nevada Mountains in eastern California western Nevada to terminate in Walker Lake, Nevada (Sharpe 2009). The headwaters of the Walker River are in montane and alpine ecosystems (Baldwin et. al., 2003), comprised mainly of subalpine forest, montane forest, and pinyon-juniper woodland (Smith 2000). Annual mean air temperatures in the lower basin range from a minimum of 5°C to a maximum of 21.6°C at lower reaches and from -4.4°C to 16.7°C at headwater sites (Sharpe 2009). Average annual precipitation at lower reaches is 127 mm, whereas headwater sites received 229 mm of precipitation annually(Sharpe 2009).

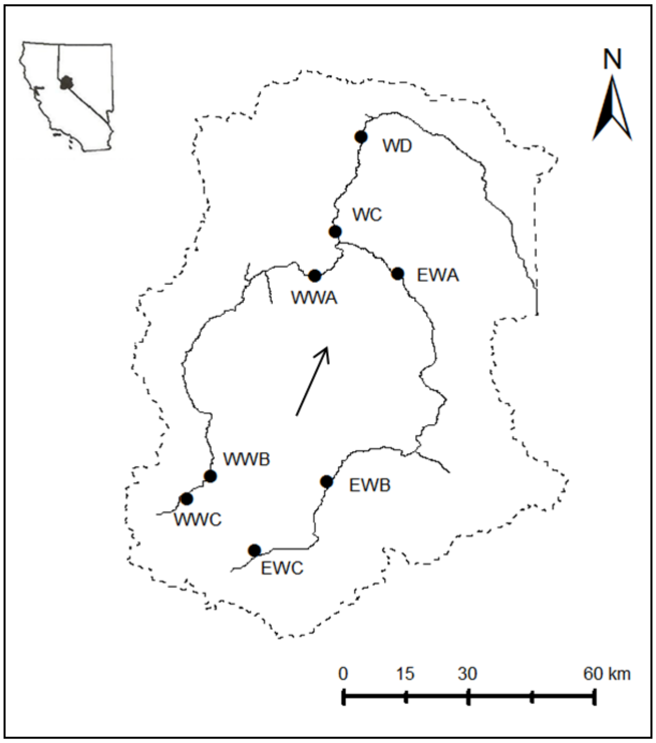

Figure 2. 1 Map of the Walker River watershed showing the eight study sites from upstream (sites EWC and WWC) to downstream site WD.Sites WWC, WWB, and WWA are located along the west fork of the Walker River; sites EWC, EWB, and EWA are located along the east fork of the Walker River and sites WC and WD are located along the main stem of the Walker River. The arrow indicates the flow direction.

For this study, eight representative sampling sites were selected along the west and east branch and the main stem of Walker River (Figure 2.1, Table 2.1). The East Walker River C (EWC) and West Walker River C (WWC) sites were at high elevations in the Sierra Nevada Mountains of California. Sites East Walker River E (EWB), East Walker River A (EWA), West Walker River A (WWA), and West Walker River B (WWB) were all located downstream (. Sites Walker D (WD) and Walker C (WC) were located along the main stem after the confluence of the east and west branches.

Table 2.1 Site codes (WWC = West Walker River C, EWC = East Walker River C, EWB = East Walker River B, EWA = East Walker River A, WWA = West Walker River A, WWB = West Walker River B, WD = Walker D and WC = Walker C), distance from the headwaters (DHW), watershed area (WSA), elevation (Elev.)

Site	DHW (km)	WSA (km^2)	Elev. (m)	Land Use (%)					
				Forest	Shrub	Agriculture	Wetlands	Urban	Other
WWC	10	2.1	2173	3	88	0	0.4	0	8.6
EWC	10	19.5	2180	34	52	0	0.1	0	13.9
WWB	46	464	2008	19	63	0	0.7	0.8	16.5
EWB	34	953	1935	24	57	0.3	1.4	0.9	16.4
WWA	98	2545	1417	17	69	4.7	0.8	1.4	7.1
EWA	85	2844	1394	29	62	0.7	1	0.4	6.9
WD	101	5810	1335	23	66	2.9	1	0.8	6.3
WC	131	6204	1320	21	67	3.7	1	1	6.3

Stream water, BMIs, seston, and periphyton were collected on three occasions from six sites in May 2010, at eight sites in August 2010, and at eight sites in September 2010 representing the spring, summer, and fall seasons, respectively. Ice and snow in May prevented sampling at the upstream sites EWC and WWC. Periphyton was not sampled at site WC throughout the study due to a sandy substrate. Water samples were collected along at each site along a transect line that was oriented perpendicular to the channel and spanned the wetted width of the river in 1 L, acid washed plastic bottles. Six BMI samples ($0.11m^2$ x $0.11m^2$) were taken at each site 2 m above the transect line using a 250µm-mesh D-frame net by disturbing the stream bottom for at least one minute. BMI were classified in the field to the lowest taxonomic level possible and functional feeding groups (FFG) were designated according to Merritt and Cummins (1996). FFG in this study included scraper (SC) (graze on periphyton), collector-gatherer (CG) (gather fine organic material) and collector-filterer (CF) (filter fine organic material). Three replicate samples (n=3) of stream seston were collected from the water column using the 250µm-mesh-size D-frame net 2 m upstream from the BMI transect line from the left and right banks, and the thalweg. Three replicate samples (n =3) of periphyton samples were collected 5 m above the BMI transect line by scraping and rinsing periphyton from three representative rocks with distilled water from the surface area. All samples were placed on ice immediately after collection and stored at -20°C until further processing.

In the laboratory, foreign material was removed by rinsing all samples in deionized water. BMI body length was measured individually with calipers and body mass determined to the nearest 0.1 mg. *Corbiculidae* tissue was separated from its shell. Seston samples were vacuum filtered through pre-weighed and pre-ashed 0.7 µm glass fiber filters (Whatman GF/F). BMI, seston, and periphyton were dried at 50°C for 72 h and ground to a fine powder using a mortar and pestle. For TP analyses small animals were pooled (2-8 organisms) to achieve the necessary sample mass of at least 200 µg. Larger invertebrateswere analyzed separately, and C, N, and P analyses were done on the same organisms. The analysis was limited to P in cases when a small amount of tissue was available. Samples were analyzed for P using the ascorbic acid method by digesting samples in potassium persulfate and sulfuric acid for 1 h at 121 °C, and P concentration was determined coloriometrically Samples were analyzed for C and N by dry combustion at 960°C using an elemental analyzer (Perkin-Elmer 2400 Series II CHNS/O Analyzer, Waltham, MA, USA) at the Goldwater Environmental Laboratory, Arizona State University. C, N, and P concentrations were calculated as percentage per dry mass (DM), and C:N, C:P, and N:P ratios were calculated based on molar units. Water samples were analyzed for TP, SRP, dissolved inorganic nitrogen (DIN), NH_3-N, DOC, and TSS at the Water Analysis Laboratory at the Desert Research Institute, Reno according to APHA standards (1992).

2.2.2 Land Use Analysis

The Walker River watershed was divided into eight sub-watersheds using ArcGIS (version 10; Environmental Systems Research Institute, Redlands, California). Land use categories were obtained from a United States Geological Survey (USGS) data set from 2006. Using the GIS database, 16 different land use classes were identified and the percentage of land use type within each sub-watershed was calculated (Table 1). Of these classes, agricultural land, urban areas, forested land, wetlands, and shrub land were selected as the primary land uses for this study.

2.2.3Data Analysis

The effects of distance from headwaters (DHW) and season on physical (temperature, flow depth, flow velocity) and chemical (DIN, NH_3-N, SRP, TP, stream water N:P, DOC, TSS) water variables were tested by using multiple linear regressions analysis (MLR) followed by corrected Akaike's Information Criterion for small samples sizes (AICc), to determine which of the predictor variables - alone or in combination - best explained dependent variables. Land use and physical and chemical water quality parameters as predictor variables in our MLR analysis followed by AICc to find the best model to explain periphyton and seston stoichiometry. One-way ANOVA was used to test for differences between periphyton and seston %C, %N, %P, C:N, C:P, and N:P ratios. MLR was used to test effects of land use, season, DHW, physical and chemical water parameter on periphyton and seston C:N, C:P, and N:P ratios followed by AIC to find the variable(s), which best predict periphyton and seston stoichiometry. MLR analysis followed by AICc was used to test which predictor variable, including season, DHW, seston and periphyton stoichiometry, and BMI body mass best predicted variation in BMI elemental composition. Data used in MLR and AICc were tested for multicollinearity by assessing r^2 and variance inflation factors for each model. Multicollinearity was not detected among the data. Differences in %C, %N, %P, C:N, C:P, N:P, and N:P imbalances were compared among the most common BMI taxa (here, families) and between FFGs followed by Tukey HSD post hoc test. One-way ANOVA was used to test for seasonal and temporal differences in %C, %N, %P, C:N, C:P, N:P of the most common BMI taxa. Elemental imbalances between food sources and BMIs were calculated for each site as shown in Elser & Hassett (1994):

$$X{:}Y_{\mathrm{Imbalance}} = X{:}Y_{\mathrm{Producer}} - X{:}Y_{\mathrm{Consumer}} \qquad \text{(eq.2.1)}$$

where $X{:}Y_{\mathrm{Imbalance}}$is the elemental producer - consumer - imbalance, $X{:}Y_{\mathrm{Producer}}$is the elemental ratio of the producer (i.e. seston and periphyton) and $X{:}Y_{\mathrm{Consumer}}$is the elemental ratio of the consumer (i.e. BMI's).

Prior to statistical analyses all data were tested for normality and homogeneity of variances using the Shapiro-Wilks and Levene's tests respectively, and log-transformed if necessary. Proportions of land use were arcsine-square root transformed. Statistical analyses were performed in JMP (Version 5.01. SAS Institute Inc., Cary, NC).

2.3Results

2.3.1 Physical and Chemical Water Quality Parameters

MLR was used including distance from headwaters and season as single predictors or both variables combined to test the effects on physical and chemical water quality parameters. AICc values were calculated to find the model which best explains the dependent variables. Results are summarized in Table 2.2. The % agricultural land, % urban areas, and % wetland increased significantly with DHW ($r^2 = 0.783$, $p < 0.001$; $r^2 = 0.456$, $p = 0.001$, $r^2 = 0.303$, $p = 0.012$). Percent forested and % shrub land were not significantly correlated with DHW. Of physical variables, flow velocity was best explained by season ($r^2 = 0.17$, $p = 0.05$) but neither explained by DHW nor by the combination of DHW and season. In contrast, flow depth was best explained by DHW ($r^2 = 0.25$, $p = 0.03$), whereas temperature was best explained by DHW ($r^2 = 0.22$,

Table 2.2 Multiple linear regressions and corrected Akaike's Information Criterion (AICc) analysis to identify the effects of distance from headwaters (DHW), season (spring, summer, and fall) and season and DHW on physical and chemical water quality parameters r^2 = regression coefficient, $*p < 0.05$, $** p < 0.001$.

	Predictor Variables						
	DHW		Season		DHW **and** Season		Order of predictor variables according AICC
Land Use Variables	r^2	AICc	r^2	AICc	r^2	AICc	
% Agriculture	0.783**						
% Forest	0.044						
% Shrub	0.001						
% Urban	0.456**						
% Wetlands	0.303*						
Temperature	0.22*	58.2	0.08	61	0.33*	58.6	DHW > DHW and Season > Season
Flow Depth	0.25*	90.9	0.04	95.5	0.28	93.7	DHW > DHW and Season > Season
Flow Velocity	0.01	141.8	0.17*	137.9	0.17	140.8	Season > DHW and Season > DHW
DIN	0.38*	120.3	0.12	127.4	0.56**	117	DHW and Season > DHW > Season
NH3-N	0.35*	39.9	0.01	48.2	0.35*	43	DHW > DHW and Season > Season
SRP	0.54**	111.3	0	126.8	0.54**	114.3	DHW > DHW and Season > Season
TP	0.57**	140.7	0.02	151.3	0.69**	137.1	DHW and Season > DHW > Season
Water N:P	0.03	58.2	0	58.8	0.04	61.2	DHW > Season > DHW and Season
DOC	0.45**	12.2	0.14	20.9	0.53**	11.9	DHW and Season > DHW > Season
TSS	0.30*	133.7	0.36*	131.9	0.56**	126.4	DHW and Season > Season > DHW

0.05). Most of the chemical variables were explained either by DHW or by the combination of DHW and season. Season as a single predictor did not explain any of our chemical water quality parameters, except TSS. However, according to AICc values, TSS was best explained by the combination of DHW and season. Among other chemical variables, NH_3-N and SRP were best explained by DHW ($r^2 = 0.35$, $p = 0.01$, $r^2 = 0.54$, $p = 0.0001$). NH_3-N ranged from 4 to 7 µg/L for upstream sites without agricultural areas and only 0.8% urban areas in the watershed and from 7 to 37 µg/L for downstream sites. SRP varied 3-fold, form 3 to 9 µg/L for upstream sites and more than 10-fold, from 10 to 105 µg/L for downstream sites. DIN, TP, DOC, and TSS were best explained by a combination of DHW and season ($r^2 = 0.56$, $p = 0.001$, $r^2 = 0.69$, $p = 0.0001$, $r^2= 0.53$, $p = 0.001$, $r^2 = 0.56$, $p = 0.0004$). Stream water N:P ratios at all sites were far below the Redfield ratio (Redfield N:P = 16) (mean = 1.6 ± 0.76), except at the upstream site WWB (N:P: 17). However, stream water N:P ratio was neither explained by DHW or season nor by the combination of both variables.

2.3.2 Basal Resources Stoichiometry

When data from all three seasons and eight sites where considered together, %N and% P of both periphyton and seston were similar, however, seston %C was significantly higher than periphyton %C (ANOVA, df = 39, p = 0.0007), resulting in higher seston C:N (20 versus 12; ANOVA, df = 39, $p< 0.0001$) and C:P ratios compared to those in periphyton (419 versus 224; ANOVA, df = 39, $p< 0.0001$).Seston N:P ratios were higher than periphyton N:P ratios, but differences were non-significant (23 versus

18; ANOVA, df = 39, p = 0.08). Both, seston and periphyton C:P and N:P ratios were significantly positively correlated (seston: $r^2 = 0.29$, $p = 0.01$; periphyton: $r^2 = 0.70$, $P < 0.0001$), indicating an intimate coupling of C and N in Walker River.

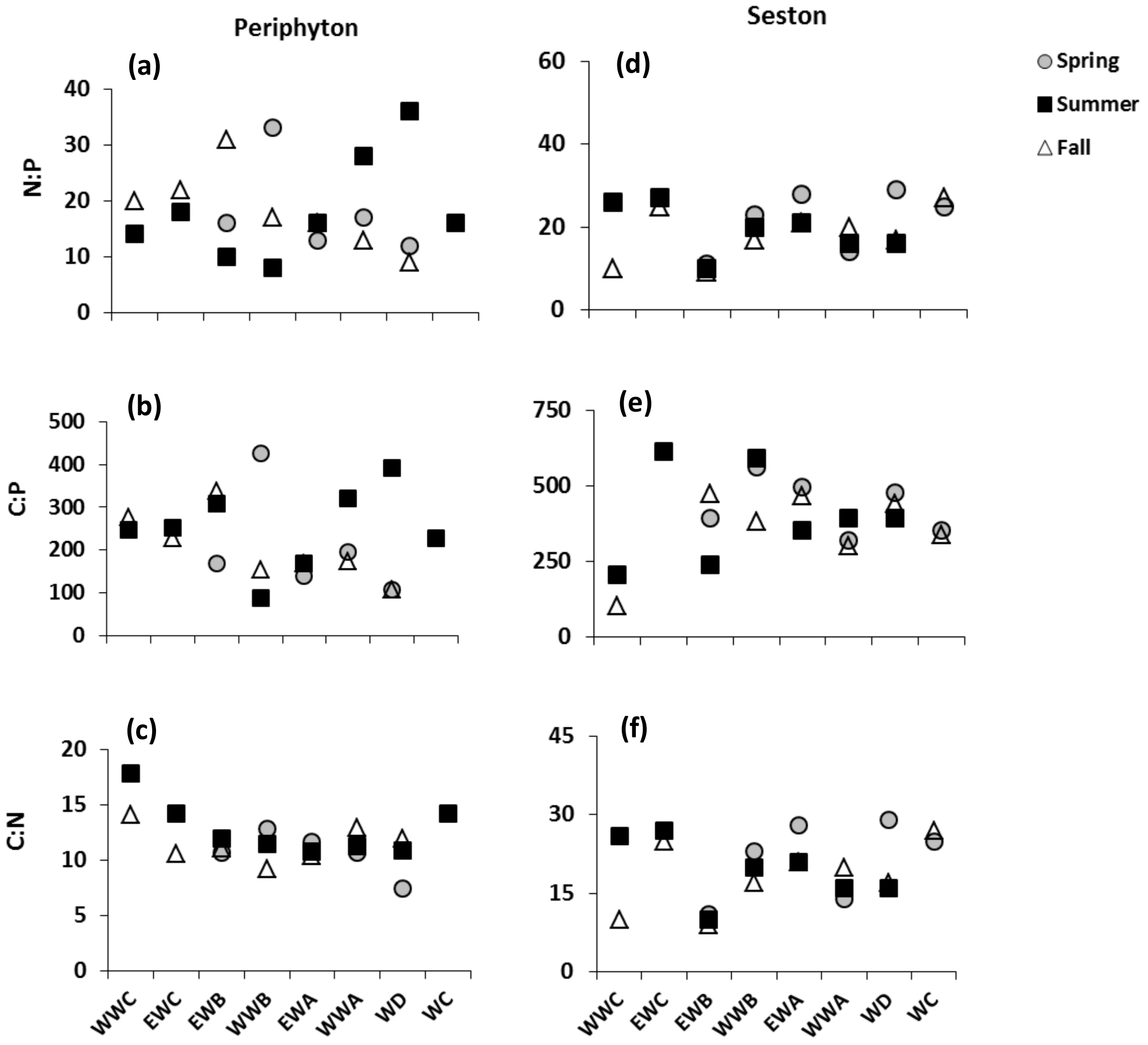

Figure 2.2 Periphyton N:P (a), C:P (b), C:N (c) and seston N:P (d), C:P (e), and C:N (f) (n =3 for all variables) from eight sites along the Walker River sampled in Spring (April), Summer (August), and Fall (September) 2010. Sites WWC and EWC were not sampled in Spring.

An indication of seasonal variability in elemental composition of periphyton and seston along the river is shown in Figure 2.2 a-f. Seston C:N ratios ranged 3-fold, from 9 to 29 (mean = 20 ± 1.4 (SE) and were more variable than periphyton (range: 7 to 18, mean = 12 ± 2.1) indicated by a higher coefficient of variation (31 vs. 18%). Seston C:P ratios ranged nearly 9-fold, from 104 to 900 (mean = 419 ± 36), whereas it was only 5-fold for periphyton C:P ratio (range: 87 to 427, mean = 224 ± 21). Similarly, seston N:P ratio ranged 6.5-fold, from 8 to 52 (mean = 23 ± 2.2), whereas the periphyton N:P ratio only varied 4.5-fold, from 8 to 36 (mean = 18 ± 1.8).

Periphyton C:N ratios were negatively correlated with % urban areas (i.e. decreased with increase of urban areas in the watershed) whereas periphyton C:P ratios were negatively correlated with DHW, and positively correlated with stream water temperature and N:P (Table 2.3). Periphyton N:P ratios were not explained by any of the predictor variables in our analysis. Seston elemental ratios were best explained by a combination of land use and chemical water quality parameters. C:N ratios were best predicted by a combination of % forested land and DOC, whereas seston C:P ratios were best explained by a combination of land use, with % wetland and % urban areas as the strongest predictors. Seston N:P ratios were best predicted by % agricultural land, DOC, and SRP.

Table 2.3Results of multiple regression analysis and Aikaike's Information Criterion identifying variable predictors of periphyton and seston elemental stoichiometry (r^2 = regression coefficient for complete model, slope indicates the direction of each of the effects on independent variable, p for each of the variables in the complete model is given).

Dependent Variable	Predictor Variable	r^2	p	Slope
Periphyton C:N	% Urban	0.21	0.041	-24.468
Periphyton C:P	DHW	0.59	0.002	-1.34
	Temp.		0.004	16.053
	stream water N:P		0.002	18.484
Seston C:N	% Forest	0.47	0.002	98.059
	DOC		0.038	-1.335
Seston C:P	% Forest	0.65	<0.001	-44.637
	DOC		0.003	1398.795
Seston N:P	% Agriculture	0.44	0.043	49.458
	% DOC		0.004	3.434
	stream water SRP		0.105	-0.178

2.3.3 Consumer Stoichiometry

The nutrient content and elemental stoichiometry of fourteen dominant BMI taxa along Walker Riveris presented in Table 2.4. The most abundant BMIs that use seston as a potential food source were Hydropsychidae and Corbiculidae (Collector-Filterer), Ephemerellidae (*Attenella*, *Ephemerella*, *Serratella*), Baetidae (*Baetis tricaudatus*), and Ameletidae (*Ameletus*) (Collector-Gatherers) and BMI's that use periphyton as a potential food source were Heptageniidae (*Cynigmula*, *Heptagenia*,*Rithrogena Epeorus*) (scrapers). Significant difference in %C, %N, %P, C:P, and N:P ratios among major BMI families (ANOVA: %C: df = 5, p = 0.0002, %N: df = 5, p = 0.0001, %P: df = 5, p = 0.0001, C:P: df = 5, p = 0.047, and N:P: df = 5, p = 0.018, Table 2.4).

Table 2.4 Mean (± SE) %P, %C, %N, C: N, C:P, and N:P of BMI taxonomic groups belonging to three functional feeding groups (FFG), SC = scraper, CG = collector-gatherer, CF = collector-filterer. (n = number of individuals to calculate the mean).

Taxon	FFG	P	C	N	C:N	C:P	N:P	n
		% of dry mass			molar			
Heptageniidae								
Heptagenia sp.	SC	0.72 (0.1)	43 (1.4)	9 (0.2)	6 (0.2)	151 (14)	27 (2.6)	17
Rhithrogena sp.	SC	0.51 (0.1)	44 (1.9)	9 (0.3)	6	236 (50)	42 (8.5)	20
Cinygmula sp.	SC	0.57 (0.01)	43 (0.6)	9 (0.27)	6 (0.04)	194 (6)	33 (0.5)	18
Epeorus	SC	0.75 (0.03)	48 (1.8)	9 (0.3)	6 (0.16)	170 (6)	30 (0.8)	22
Ameletidae								
Ameletus sp.	CG	0.73 (0.07)	46 (1.6)	8 (0.6)	7 (0.7)	190 (24)	29 (4.2)	91
Baetidae								
Baetis tricaudatus	CG	0.85 (0.1)	46 (1.4)	8.2 (0.5)	7 (0.4)	154 (21)	24 (3.6)	115
Ephemerellidae								
Attenella sp.	CG	0.8 (0.13)	46 (0.16)	10 (0.19)	6	156 (28)	28 (5.22)	13
Ephemerella sp.	CG	0.65 (0.04)	50 (3.4)	7 (0.62)	10 (1.3)	213 (21)	24 (3.37	34
Serratella sp.	CG	0.75 (0.05)	45 (1.70	10 (0.31)	6 (0.2)	154 (12)	27 (2)	23
Hydropsychidae								
Hydropsyche	CF	0.74 (0.04)	48 (1.2)	8 (0.3)	7 (0.4)	173 (7)	28 (1.8)	67
Corbiculidae								
Corbicula fluminea	CF	0.53 (0.1)	38 (2)	6 (0.3)	7 (0.3)	210 (22)	29 (2.3)	30

C:N ratios were not significantly different between BMI families(Table 2.5). *Corbiculidae* were generally lower in %C, %N, and %P than other families. *Baetidae* were richer in %P and *Heptagenidae* were richer in %N compared to other families. *Baetidae* had lower C:P and N:P ratios than other families. When separated by FFG's, %P was significantly higher in CG compared to other FFGs (ANOVA, df = 2, p = 0.021, Table 2.5), whereas %N was higher in SC (ANOVA, df = 2, p = 0.0018). Consequently, SC C:N and N:P ratios were significantly lower and higher, respectively compared to other FFGs. (ANOVA, C:N: df = 2, p = 0.029; N:P: df = 2, p = 0.047). No significant differences were found in C:P ratios among FFGs.

Table 2.5 Analysis of variance results for the differences in %P, %C, %N, C: N, C:P, N:P, and N:P consumer-resource imbalances among the six benthic BMI families and among three functional feeding groups (FFG). Different letters indicate significant differences between FFG's and families. SC = scraper, CG = collector-gatherer, CF = collector filter, AMEL = Ameletidae, BAET = Baetidae, CORB = Corbiculidae, EPHE = Ephemerellidae, HEPT = Heptageniidae, HYDR = Hydropsychidae.

Variable	Differences among FFG's	F	p	Differences among Families	F	p
%C	n.s.			HYDR^{a} > EPHE^{a} > BAET^{a} > AMEL^{a} > HEPT^{a} > CORB^{b}	5.6325	0.0002
%N	SC^{a} > CG^{a,b}>CF^{b}	6.765	0.001	HEPT^{a} > AMEL^{a} > HYDR^{a} > BAET^{a} > EPHE^{a} > CORB^{b}	5.6811	0.0001
%P	CG^{a} > SC^{a,b} > CF^{b}	4.058	0.021	BAET^{a} > HYDR^{a,b} > EPHE^{a,b} > AMEL^{a,b} > HEPT^{a,b} > CORB^{b}	7.7928	0.0001
C:N	CF^{a}>CG^{a}>SC^{b}	3.701	0.029	n.s.		
C:P	n.s.			CORB^{a} > AMEL^{a,b} > HEPT^{a,b} > EPHE^{a,b} > HYDR^{a,b} > BAET^{b}	2.3579	0.047
N:P	SC^{a}> CF^{a,b}>CG^{b}	3.1642	0.047	HEPT^{a} > CORB^{a,b} > HYDR^{a,b} > AMEL^{a,b} > EPHE^{a,b} > BAET^{b}	2.8903	0.018

The variables predictors that best explained the elemental stoichiometry of the most common BMI taxa are presented in table 2.6. The %N and consequently C:Nin *Ameletidae* were best explained by season and seston C:N ratio ($r^2 = 0.73$, $p = 0.005$), with significantly lower C:N ratios in summer compared to spring. *Baetidae* C:N, *Serratella* C:P, and N:Pwere best predicted by body mass. *Ephemerella* C:N and C:P ratios were best predicted by seston %C and %P. By considering site and season separately, %P in *Corbiculidae* was significantly higher at downstream sites (ANOVA, df = 1, $p = 0.005$) and consequently the C:P ratio (ANOVA, df = 1, $p = 0.03$) and the N:P ratio (ANOVA, df = 1, $p = 0.036$) were significantly lower compared to those sampled at upstream sites. C:N ratios in *Hydropsyche* were significantly higher in spring compared to summer and fall (ANOVA, df = 2, $p < 0.001$).

Table 2.6 Results of multiple regression analysis and Akaike's Information Criterion analysis identifying stream variables that best predict BMI elemental stoichiometry (r^2 = regression coefficient for complete model, slope indicates the direction of each of the effects on independent variable, p for each of the variables in the complete model is given).

Dependent Variable	Predictor Variable	r^2	p	Slope
Ameletus C:N	Season	0.73	0.087	-0.868
	Seston C:N		0.013	-0.182
Baetidae C:N	Body Mass	0.61	0.001	0.751
Serratella C:P	Body Mass	0.74	0.013	-28.584
Serratella N:P	Body Mass	0.72	0.016	-4.267
Ephemeralla spp. C:N	Seston %C	0.66	0.008	0.812
Ephemeralla spp. C:P	Seston %P	0.49	0.036	1142.27

2.3.4Consumer-Resource Imbalances

Elemental imbalances were apparent in all FFG’s and no clear spatial trend was observed between nutrient-rich and nutrient-poor sampling sites. However, imbalances in scraper tend to decline with increasing SRP and DIN concentration downstream. Also, imbalances in C:N between scraper and periphyton were lower compared to those between collector-gatherer, collector-filterer and seston. Imbalances in C:N between collector-gatherer, collector-filterer and seston were close to zero at site EWB, which had the highest DIN and SRP concentration of all sampling sites over the study period.

Imbalances in C:P were variable and lower for scraper compared to collector-gatherer and collector-filterer and tended to decline downstream with increasing levels of SRP. Imbalances between FFG’s and their potential food source were negative, except at site EWB, indicating that BMI in Walker River are rather N-limited. Imbalances were higher for scraper and lower for collector-gatherer and collector-filterer. Although an increase in SRP and DIN was observed form upstream to downstream parts of Walker River no trend was observed in the N:P imbalance for any of the FFG’s.

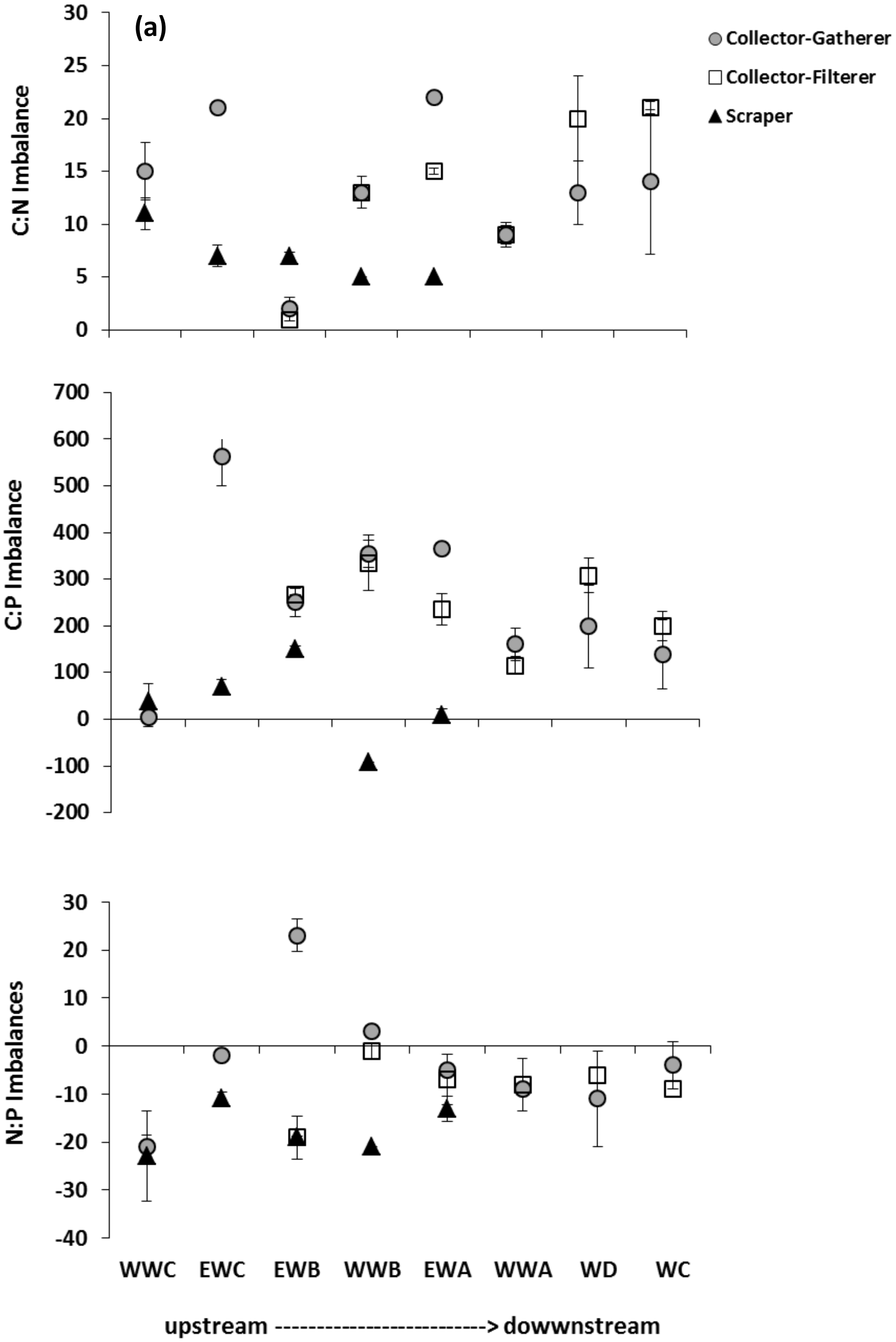

Figure 2.3 Calculated C:N (a), C:P (b), and N:P (c) imbalances (± SE) between collector-gatherer (CG), collector-filterer (CF), and scrapers (SC) and basal resource along the river Consumer-resource C:N, C:P, and N:P imbalances from all three seasons were pooled. Scrapers were not found at sites WWA, WD, and WC and collector-filterers were not found at sites WWC and EWC.

2.4Discussion

2.4.1 Land Use Variables and Water Quality Parameters

Among the land use variables we used in our study, % urban areas, % agricultural and wetland increased significantly along the flow path of the Walker River. By using DHW (as a proxy variable for changes in land use) and season as predictor variables, we determined which variable as a single or combined best explained our physical and chemical water quality parameter. Including season as second variable is essential when studying effects of land use on water quality. For example TP or DIN was not significantly related to increase in agricultural and urban land along the river gradient.

However, by taking seasonal effects into account, TP and DIN as well as DOC and TSS were best explained by multiple effects of DHW and season. TP and DOC showed higher values during summer and fall season. This is most likely due to an increase in agricultural, urban development, and wetland areas (i.e. DHW-effect) and an increase of agricultural activities during the growing season (i.e. seasonal effect). However, DOC in stream water was highly correlated with % of wetlands in the watershed. Wetlands are known for the export of dissolved carbon and the retention of other nutrients (Wetzel 2001). These results support findings from Laudon et al. (2011) who showed that DOC dynamic is regulated by the combination of hydrologic pattern and the proportion of wetlands in the watersheds. The smaller DOC concentrations in our study (0.2 -7 mg/l) compared to those from Laudon et al. (2011) (2-47 mg/L) is likely caused by smaller proportion covered by wetlands in our study. The range and concentration of SRP in Walker River (4 to 105µg/l) was higher than those from a temperate stream affected by agriculture and urbanization (e.g. Harding et al. 1999, O'Brien and Wehr 2010, Tsoi et al., 2011). However, Allan (2004) showed that streams in agricultural watersheds remain in good condition until the extent of agricultural land comprises more than 30- 50% of the watershed. However, urban and agricultural land can have a disproportionately large influence over distance (Paul & Meyer, 2001; O'Brien and Wehr, 2010). This is likely the case in the Walker River watershed. The proportion of agricultural and urban development in each of our eight sub-watersheds was small (0-4.7%) compared to % shrub land and % forested land (57-88% and 3-34%, respectively).

However, the cultivation of fertilizer-intensive crops in close proximity to the river channel is likely responsible for higher nutrient concentrations downstream during growing season. Based on the study along a New Zealand stream affected by long-term agricultural activities, Harding et al. (1999) concluded that intensity and duration of agricultural activities rather than the percentage of agricultural land in a watershed can be a better indicator to assess impacts on river health.

Other variables, such as temperature, flow depth, NH_3-N, stream water N:P, were best explained by DHW only and seem to be less effected by season in Walker River. The N:P ratios in our study were low (taking the Redfield ratio of 16 as a reference value) except for the upstream WWB site during spring, which is unaffected by water diversions or upstream influences of agriculture (Sada et al., 2009). In our study, DIN concentration was lower than SRP concentration along the entire Walker River in spring and summer. One explanation might be a faster uptake of nitrate than SRP by primary producers which results in very low N:P ratios similar to those in a hot desert stream in Arizona (Grimm and Fisher, 1986; Grimm 1988).

2.4.2 Elemental Stoichiometry of Basal Food Sources

Elemental ratios of basal food resources reflected spatial and seasonal differences in the Walker River watershed (Figure 2, Table 3). Results support our assumptions, that elemental ratios of basal food resources are affected by the combination of multiple factor rather than by single variables. Nutrient stoichiometry of seston and periphyton was best predicted by land use-associated differences in physical and chemical water quality parameters. The effect of seasonal application of fertilizers by agriculture and urbanization on elemental ratios of basal food resources were in parts confirmed in our regression models (Table 2.3). We found a relatively weak negative relationship between periphyton C:N ratios and % of urban development, probably caused by export of nutrients bound on soil particles or dissolved nutrient (Jarvie et al., 2008). Periphyton C:N and C:P ratios in this study were higher and within the same range, respectively than those found in streams within an urban-rural land use gradient in New York State (O’Brien and Wehr, 2010). Variation of periphyton C:P (87-427) and N:P ratios (8-36) in our study were partly predicted by stream temperature and stream water N:P ratios. The combination of temperature-related nutrient uptake and nutrient limitation (indicated by stream water N:P ratios) appear to be an explanation for these patterns (Bothwell 1985, Stelzer and Lamberti 2001). Considering the low stream water N:P ratio, we expected periphyton to be N- limited seasonally and spatially. Nitrogen limitation has been reported when ambient nitrate-N concentration ranged between 18 to 55μg/l, where N:P ratios ranged between 1.6 to 2.6 in a desert stream in Arizona (Grimm and Fisher 1986). In the Walker River, stream water N:P ratios were approximately in the same range. Only in fall, was the DIN concentration of 55µg/l and consequently N:P ratios exceeded at thedownstream sites. In contrast, the predicted SRP concentration of 16 µg/l from maximal algae growth experiments (Rier and Stevenson2006) was exceeded at the downstream sites during all season. Kahlert (1998) considered benthic algae N:P ratios greater than 32 to be P-limited, and N:P ratios less than 12 to be N- limited. At only two sites in our study were periphyton N:P ratios below 12, and at only one site above 32, whereas most N:P ratios indicated either N or P limitation.

Seston elemental ratios in our study were higher than those reported from northern Michigan streams (Frost et al., 2009), but seston C:N ratios were within the range of those observed in a Coastal Plain stream in Georgia (Atkinson et al., 2009). However, the elemental composition of basal food resources could not fully be explained by agricultural and urban land, indicating there may be other factors affecting seston and periphyton nutrient stoichiometry. Seston C:N stoichiometry was positively related to the % of forested land. In highly forested areas, allochthonous material is composed of C-rich and nutrient-poor material, such as leaf litter and wood (e.g. Sterner and Elser, 2002) assuming that seston along upstream sites of Walker River was comprised of mostly allochthonous material particularly during the fall season. Consequently, differences in seston C:N and C:P ratios between upstream sites WWC and EWC (Figure 2 d-f) may be attributed to differences in % forested land, which varied between 3% (WWC) and 34% (EWC). In accordance with Frost et al. (2009), seston C:P ratios in our study were also positively related to the % of wetlands (indicated by DOC). One explanation is that wetlands can alter the quality of seston by retaining nutrients and releasing DOC in the receiving stream (Wetzel 2001). Seston N:P ratios were best predicted by a combination of agriculture, DOC and SRP. The % of agricultural land and seston N:P ratios were negatively correlated in our study, indicating an stronger effect of DIN input due to life stock grazing rather than crop farming (P-rich fertilizer) on seston N:P ratios.

Hydrological modifications due to dams and reservoir along the Walker River might also have an effect on the elemental composition of basal food resource. Hydrological conditions and watershed discharge can influence seston elemental ratios by increasing the amount of nutrient-rich particles from adjacent floodplains during high flow events (Atkinson et al., 2009; Frost et al., 2009).Upstream lakes can release N-rich particles to outflowing streams resulting in high amounts of authochthonous matter in the seston pool (e.g. Whiles and Dodds, 2002; Frost et al., 2009). The inflow of seston particles from Bridgeport Reservoir was most likely the reason for low seston C:N ratios at mid-reach site EWB. Seasonal differences in stream discharge can be an important predictor to assess relationships between seston elemental composition and watershed properties (Frost et al., 2009). We found seston C:N ratios were negatively related to stream discharge in spring and summer. Frost et al., (2009) found that the variability of seston C:N and C:P ratios could be explained by % wetlands and % agricultural land, respectively during high flow conditions. Similarly, Atkinson et al. (1999) observed a negative relationship between seston quality and flow conditions in a Georgia watershed when the stream was connected to the flood plain.

2.4.3 Elemental Stoichiometry of Benthic Macroinvertebrates

BMI’s showed considerable variation in nutrient content and in elemental ratios (Table 2.4, Table 2.5). One-way ANOVA revealed significant differences among FFGs and among families. Among insects, %P was more variable that %C and %N and consequently led to differences in C:N, C:P, and N:P ratios among insects. However, differences were not significantly different, except for N:P ratios, which was significantly higher in Heptagenidae compared to those in Baetidae. In contrast, Corbiculidae had significantly lower %C and %N compared to insects. Taxonomic differences have been shown to be a strong predictor of nutrient content and elemental ratios in BMI (Liess andHillebrand, 2005), mostly attributed to differences in major biomolecules due to growth rate-related allocation of P-rich ribosomal RNA (Sterner andElser, 2001) or calcified structures (Evans-White et al., 2005). Seston and periphyton quality in our study was quite variable and elemental composition of FFGs was not explained by food quality.

However multiple regression analysis and AICc revealed that body elemental composition of *Ameletus* and *Ephemerella* were best explained by the combination of season and food quality. Interestingly, *Ephemerella* C:P ratios were negatively related to seston %P, which is in contrast to other studies (e.g. Frost andElser, 2002, Small andPringle, 2010). One possible reason is that greater %C allocation due to enhanced growth by feeding on P-rich seston offsets higher body %P (high allocation of rRNA) and consequently lead to higher C:P ratios in *Ephemerella* in our study. *Serratella* C:P and N:P ratios were significantly negative to body mass supporting the growth rates hypothesis (Sterner & Elser, 2002). The allocation of P-rich ribosomal RNA is related to higher growth rates smaller in organisms and can consequently lead to lower C:P and N:P ratios (Sterner & Elser, 2002). *Hydropsyche* showed significant spatial variation in %N between sites, which was significantly related to seston %N. Among 35 streams in Michigan and Wisconsin, Evans-White et al. (2005) also found significant spatial differences in %N of *Helicopsyche beorealis*, but not for any other BMI taxa. Cross et al., (2003) found *Trichoptera* C:P ratios were significantly lower in P-enriched streams compared to reference streams. Furthermore, *Hydropsyche* sampled in spring had significantly higher C:N ratios than in summer and fall. One can question whether or not species belonging to the order *Trichoptera* are particularly sensitive to changes in basal food sources. Further research is needed to examine the elemental composition of *Trichoptera* species, since this order is an important food source for higher trophic levels in many freshwater systems.

The C:P and N:P (but the not the C:N) ratios among FFGs in this study were low compared to those from detritus-based streams (Cross et al., 2003) and from insects in temperate streams in Michigan and Wisconsin (Evans-White et al., 2005), but within the range of those reported from oligotrophic and eutrophic Canadian lakes (Frost et al., 2003) and from a nutrient-enriched temperate stream in Great Britain (Lauridsen et al., 2012). Previous research has shown that FGGs can differ in their elemental composition. SC in our study had significantly higher %N and lower C:N ratios compared to other FFGs. This might be explained by differences in food quality; periphyton C:N ratios in our study were almost twice as low compared to those of seston. Lauridsen et al (2012) concluded that some variation in elemental ratios of BMIs can be attributed to diet. By feeding on low quality food over evolutionary time scales, herbivores might become less dependent on N (Fagan et al., 2002). These results furthermore support recent findings that consumers can deviate from strict homeostasis when feeding on food differing in quality (e.g. Bowman et al., 2005; DeMott andPape, 2005; Small andPringle, 2010).

N:P imbalances among FFGs in our study were in the range of those found by Lauridsen et al. (2012) and Bowman et al. (2005) for a nutrient-enriched temperate stream and for sites upstream of wastewater treatment plants in Rocky Mountains streams, respectively but lower than those from detritus-based temperate streams (Cross et al., 2003). We expected FFGs to be less constraint by food quality at lower reaches of Walker River due to increase of % urban and % agricultural land and associated higher nutrient inputs.

2.4.4 Consumer-Resource Imbalances

Contrary to the expectation consumer-resource imbalances would be lower at nutrient-rich downstream sites was not confirmed by the data. Although, consumer-resource imbalances were significantly different among FFGs (Table 2.5), we did not find consumer-resource imbalances to be related with DHW. In a nutrient-enriched stream in England, consumer-resource imbalances were still evident, although SRP and total oxidizable nitrogen concentration in that study was approximately four times and > 200 times higher, respectively (Lauridsen et al., 2012). Although the elemental composition of seston and periphyton can provide a rough idea about the nutritional status of a food source, Klausmeier et al. (2004) emphasized the different elemental compositions of various materials in the seston pool. Elemental imbalances should be used with caution to make predictions about elemental constraints on growth and reproduction. BMI might feed more selectively on particular parts of basal resources or dampen low quality food by compensatory feeding (Evans-White et al.; 2005 Fink and Ehlert, 2006).

2.5Conclusion

This study described the linkages between basal food resources and benthic macroinvertebrates along a gradient of land use in the Walker River watershed using elemental stoichiometry. Agricultural, urban and wetland areas increased downstream as well physical and chemical water quality parameters, such as water temperature, TSS, DIN, TP SRP and DOC. Multiple regression analysiscoupled with Aikaike’s Information Criterionseemed to be an effective approach to assess the best combination of key predictor variables that explain elemental stoichiometry of basal food resources and BMI in Walker River. The elemental composition of the basal food resources were related to land use.Periphyton C: nutrient ratio was related to the percentage of urban area, temperature, and the N:P ratio of stream water, whereas seston elemental ratios were rather related to the percentage of forested areas and DOC.Land use analysis also indicated that the percentage of a certain land use in Walker River watershed might be less important rather than the distance to the stream.

The elemental composition of BMI varied less and was explained differences in body size and also by the elemental composition of their potential food source. Thus, land use can affect trophic relationships in the Walker River by altering the elemental composition of basal food resources due to nutrient enrichment. However, clear spatial pattern in elemental imbalances in FFG’s were obscured due to high temporal variability in food source elemental composition. Applying ecological stoichiometry can be useful indicator to better understand food web dynamics in semi-arid watersheds with highly variable physiochemical conditions that such as Walker River.

CHAPTER 3

BENTHIC MACROINVERTEBRATE COMMUNITY STRUCTURE AND SECONDARY PRODUCTION, DENSITY AND BIOMASS ALONG GRADIENTS OF HYDRAULIC, TEMPERATURE AND SUBSTRATE CONDITIONS IN WALKER RIVER

Abstract

The community composition and production of benthic macroinvertebrates (BMIs) have become essential tools in stream restoration and provide valuable information about the current ‘health’ state of a stream or stream reaches. In this study BMI samples and data on substrate and hydrologic-parameters were collected bi-monthly from spring to late summer 2010 along the Walker River to assess temporal variability and BMI structure (biodiversity, density, and biomass). According to biotic indexes, downstream parts of Walker River seem less affected by anthropogenic disturbances compared to upstream reaches. Benthic invertebrate biomass varied temporally and spatially and appears to be positively related to substrate and stream temperature.

Further, secondary production of *Baetis*, one of the most common genera in Walker River was estimated between two physically and hydrologically similar sites differing in water quality to assess effects of nutrient enrichment on *Baetis* density, biomass and secondary production. Although mean individual body mass of *Baetis* was lower at the nutrient enriched site, secondary production was higher most likely due to the combination of higher growth rates and higher densities. Present findings suggest that anthropogenic impacts, such increased nutrient inputs and water withdrawal negatively

affect BMI communities in Walker River. Results from this study will be useful as a baseline data in the proposed restoration activities in Walker River, such as an increase of discharge. To prove effects of stream restoration on BMI communities long-term monitoring and localization of accurate undisturbed reference sites are required. This will also help to discriminate more accurately natural from anthropogenic effects on benthic macroinvertebrates in Walker River.

3.1 Introduction

The Walker 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(Horton, 1996). 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 (Delong and Brusven, 1998).The proposed acquiring of 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. 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).

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 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 (Ortiz and Puig, 2007), their composition changes quickly in response to environmental conditions and the magnitude of its influence on river health can be readily assessed (Bustoz-Baez and Frid, 2003). 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 (Tate and Heiny, 1995; Delong and Brusven, 1998; Rempel et al., 2000). Little is known about benchmarks for these aquatic systems where communities occupy naturally harsh environments created by high summer temperatures and low base flow.

Another helpful tool in the field of ecological integrity of stream ecosystems is secondary production (Benke 1993). 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 a certain 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/area) and production is the accrual of biomass of an organism or a population over a certain time period per unit area (mass/area.time). The Production/Biomass (P/B) ratio provides a comparison of growth rates of species between 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 an organism’s life history patterns strongly depend 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, biomass, density and secondary production of stream invertebrates increases downstream follow a strong longitudinal gradient caused by changes in stream size, resource availability, and temperature (Vannote et al., 1980). However, anthropogenic impacts can alter this longitudinal relationship. Consequences of changes in secondary production on ecosystems processes are complex and not fully understood. 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. These alterations in community structure in turn are expected to offset increased production for higher trophic levels by increasing the amount of unpalatable taxa and consequently reduce the production of top predators (Wootton and Power 1993; Davis et al., 2010). A greater understanding of anthropogenic impacts on invertebrate biomass and secondary production is necessary to fully understand implications for higher trophic levels and other ecosystems services. Assessments of BMI density, biomass and secondary production in streams in semi-arid regions particularly those related to anthropogenic induced alterations are not very frequent (e.g. Jackson and Fisher, 1986; Gaines et al., 1992). BMI community composition and secondary production has not been well studied in Walker River.

The objectives of this study is to link BMI diversity, BMI biomass and secondary production to habitat characteristics (stream flow, water temperature, sediment) to assess the ecological health of Walker River. The results provide a basis to (a) determine the most important habitat parameters affecting ecological health in the Walker River watershed, (b) assess the amount of BMI biomass available for higher trophic levels to maintain viable fish populations along Walker River, (c) improve the understanding of anthropogenic impacts onsecondary production and, (d) develop and conduct management strategies (e.g. Ecological Acceptable Flows) for the Walker River restoration goals based on the results from this study.

3.2 Material and Methods

3.2.1Study Sites

Present research was conducted at five sites along the east and west fork and the main stem of the Walker River (Figure 3.1). Two sites (WWB and WWA) are located at the west fork of Walker River, one site is located at the east fork of Walker River (EWB) and two sites are located along the main stem after the confluence of both forks. The discharge (Figure 3.2a) and the stream temperature (Figure 3.2b) were recorded at site WC for the sampling period from April through September 2010.

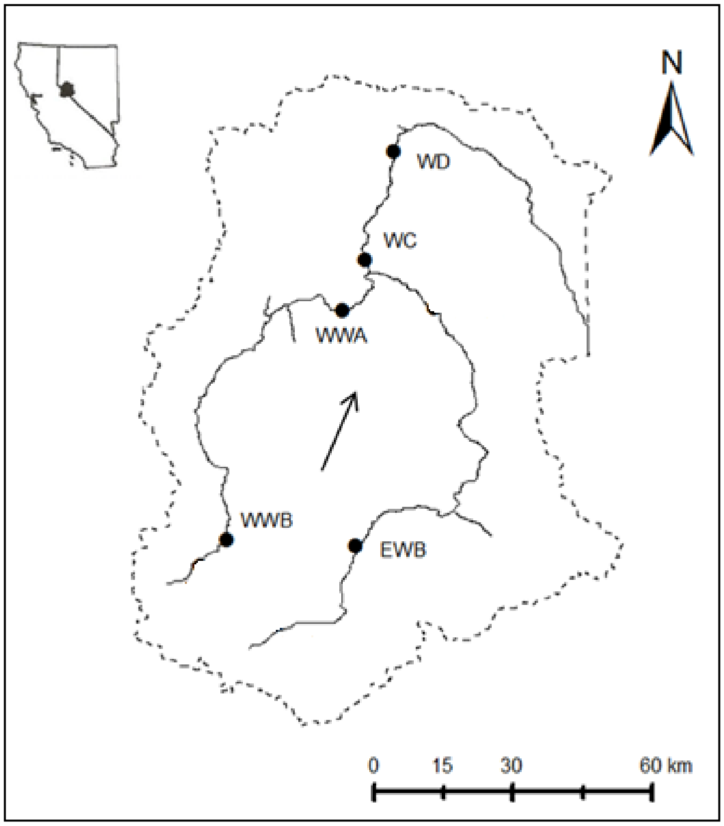

Figure 3.1 Walker River Basin and the location 2010 BMI, water chemistry, and physical habitat sampling sites. WC = Walker C; Walker D; WWA = West Walker A, EWB = East Walker B; West Walker B.

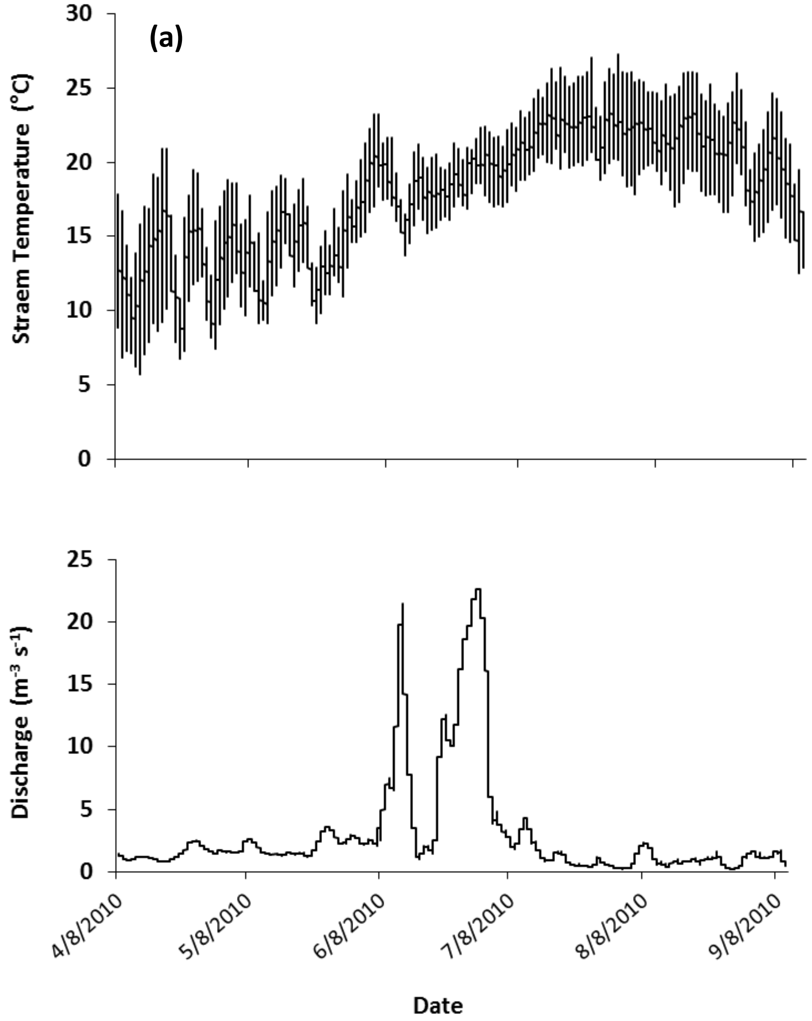

Figure 3.2: Mean daily stream temperature (a) and mean daily discharge (b) at downstream site WC for the sampling period from April through September 2010.

3.2.2Sampling and Analyses

Physical and Water Quality Sampling

Physical and chemical characteristics of the river environment were sampled at each site to quantify features that are most important to BMIs. Physical habitat characteristics were determined along transects that spanned the wetted width, and included 25cm 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 1ft^2 area that was centered on each depth/velocity point (Table 3). Water temperature was measured at 15 minute intervals from March through September using Hobo® Water Temp Pro Loggers. Water samples were collected during BMI sampling and habitat surveys. Water samples were analyzed at the Desert Research Institute Analytical Chemistry Laboratory for SRP, total nitrogen, NO_2-N, NO_3-N, NH_3-N, and TSS concentrations were measured following standard methods (APHA, 2005).

Benthic Macroinvertebrate Sampling

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% ethyl alcohol, and returned to the laboratory for processing. In the laboratory, composite samples were sub-sampled by plankton splitter and BMI's 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% (>15 organisms) of any one sample after the counts were standardized to 300. Rare taxa were not used in the analysis. For secondary production assessment, the mayfly *Baetis*spp. was used due to its high abundance during the sampling period that allowed secondary production comparison between two sites (EWB and WWB) differing in water quality. Individual organisms were placed in a white pan after collection individual body lengths were taken immediately in the field by using a microscope. Individual organisms were then placed into vials, placed on dry ice during transport and stored in the -20°C freezer until needed.

3.2.3Data Analyses

Biotic Indices

To assess temporal and spatialchanges in BMI biodiversity,species richness and species evenness among sampling sites biotic indices were calculatedusing Shannon-Wiener Index, Margelef's Diversity Index, and Pielou Evenness Index. Additionally, the Hilsenhoff Biotic Index (HBI) was used to assess the proportion pollutant-tolerant and pollutant-intolerant species in each BMI community at each sampling site.

HBI

The HBI 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. Communities in polluted or harsh environments are indicated by high HBI values and low values are indicative of communities in high quality environments. Hilsenhoff index HBI was calculated by:

$$HIB = \frac{n_i a_i}{N} \qquad \text{(Eq. 2.1)}$$

Where $n_i$is the numer of 'i'th taxon, $a_i$is the tolerance value (TV) of taxon'i' and N is the total number of species in the sample. HBI values range from zero (BMI communities in high quality environments) to 10 (BMI communities in low qualityenvironments) (Hilsenhoff, 1987).

Shannon-Wiener Index

The Shannon-Wiener Index was used to describe the diversity of BMI communities between various habitats along Walker River and was calculated by:

$$H= -\Sigma\, p_i \ln p_i \qquad \text{(Eq.2.2)}$$

where p_i is S/N, S is the number of individuals of 'i'th species and N is the total number of species in the sample and ln is the natural logarithm. The Shannon diversity index ranges from 0 to 5 and values are usually between 1.5 and 3.5. Highervaluesindicatehighercommunity complexity (Shannon, 1948).

Margalef's Index

The Margalef's Index (Margalef 1958) was used to describe the species richness of BMI communities along the Walker River:

$$\text{Margalefs Index} = (S-1)/\ln N \qquad \text{(Eq.2.3)}$$

where S is the total number of species, N is the total number of individuals in the sample and ln is the natural logarithm. The Margalef's index value depends on the numbers of species, where higher values indicate higher species richness.

Pielou Evenness Index

To assess how evenly species were distributed at each site along Walker River, Pielous' Evenness Index (Pielou, 1966) was calculated by:

$$e = H/\ln S \qquad \text{(Eq.2.4)}$$

where H is the Shannon-Wiener- Index, S is the total number of species in the sample and ln ist the natural logarithm. The values range between 0 and 1. Values close to 1 indicatean evenlydistributionof individuals in the BMI community.

BMI Density and Biomass

Density of BMI (individuals per m^2) for each sampling site was quantified by counting the number individuals collected from six sample units (0.54 m^2) taken along the transect and BMI biomass (mg m^2) was calculated by summing the oven-dried individual body mass of the same organisms.

Baetis Secondary Production Assessment

Forsecondary production assessment*Baetis*mayflies were 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 separately for *Baetis*collected from site EWB and WWB (Figure 3.1) and one-way ANOVA was used to compare body mass of *Baetis* between both sites, andp-values

<0.05 were considered significant. The size frequency distribution (Hynes &Coleman 1968) was applied to categorize the samples 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 (here, individuals of same age). 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 (see Table 3.1). Cohort production P is the sum of the last column and annual Production (P)/Biomass (B) 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.Based on previous studies (Henneberry, 2009), development time of *Baetis* in Walker River was estimated to be 5 months. 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 3.1 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

3.3Results

3.3.1 Physical and Chemical Parameters

No clear trend was found in discharge and the distance from headwaters and among sites. Mean discharge was variable among sites with the lowest value measured at downstream site WC and highest value measured at site EWB. Mean water temperatures were similar among sites (ANOVA, $p > 0.05$), except for site WWB had the lowest temperature. Mean SRP and DIN were highest at site EWB due inflow of point source pollution from Bridgeport Reservoir and lowest at site WWB, however due to small sample size differences among sites were not significant for both parameter. TSS was highest at downstream site WD and lowest at sites EWB and WWB however results were not significant.

Table 3.2 Mean and range (in parentheses)of physical and chemical variablesmeasured at five sampling sites along Walker River in April, August and September 2010.

Variable	WWB	EWB	WWA	WD	WC
Discharge (m^3s^{-1})	3.09 (1.28-4.52)	4.91 (3.29-6.74)	5.47 (4.13-7.89)	4.5 (1.59-6.51)	1.51 (1.01-2.18)
Stream Width (m)	24 (18.4-28)	21.9 (18.9-24)	21 (20.9-21)	14.8 (14.6-14.65)	7.6 (6-10.3)
Stream Depth (cm)	31.1 (24-38.7)	36.1 (25.6-49.2)	37.9 (36.3-37.2)	54 (51.1-55.4)	32.9 (23.5-40.2)
Water Temp. (°C)	9.6 (0.2-21.7)	15.6 (2.73-34.4)	16.6 (6.0-24.9)	18.5 (7.5-27.3)	18.2 (5.8-27.8)
TP (µg l^{-1})	29 (13-61)	89 (38-92)	76 (41-102)	101 (67-129)	80 (74-89)
SRP (µg l^{-1})	7 (3-9)	58 (10-105)	28 (22-31)	38 (33-48)	42 (35-52)
DIN (µg l^{-1})	12 (5-24)	68.7 (7-108)	35.7 (22-55)	48.7 (34-73)	34.3 (10-71)
TSS (mg l^{-1})	16.8 (2-41)	5.1 (3.4-6)	29 (7.4-43.4)	41.7 (18.6-62)	20.7 (12-27.8)
Substrate (mm)	93 (0.1-450)	69.5 (0.1-400)	62.0 (0.1-380)	23.4 (0.1-400)	2.8 (0.1-25)

3.3.2 Benthic Macroinvertebrate Biodiversity along Walker River

A total of 1816 individual BMIs were identified from 60 taxa in 15 samples. Many of these taxa rarely occurred in all the samples. Only a few taxa were common to all the sampling sites and occasions. The BMI fauna was dominated by the genus *Baetis*, *Ephemerella*, *Isoperla*, *Rithrogena*, *Serratella*, *Ameletus*, and *Heptagenia*, and combined, constituted 68% of the total biomass. The remaining 30 taxa were found irregularly during the investigation and in small numbers. Rare taxa were defined as all taxa that did not total more than 50 organisms in all samples combined, or more than 5% (>15 organisms) of any one sample after the counts were standardized to 300.

Diversity indices indicated spatial and temporal shifts in the species composition along Walker River. Margalef's (Figure 3.3a) and Shannon Wiener index (Figure 3.3b) indicated that species richness decreased downstream towards species-poor assemblages with few dominant taxa. Evenness of community composition indicated by Pielou's (Figure 2.3 c) seem to be less affected and no clear trend was found between the indexes and the distances to headwater. However, Pielou's index is sensitive to the sample size, causing the very high values at site WD despite low species diversity and richness values at this site. Interestingly, there was a large temporal change in Simpson's diversity index at site EWB (range: 0.36-0.78), whereas at site WWB the change was small between seasons (range: 0.86-0.93).

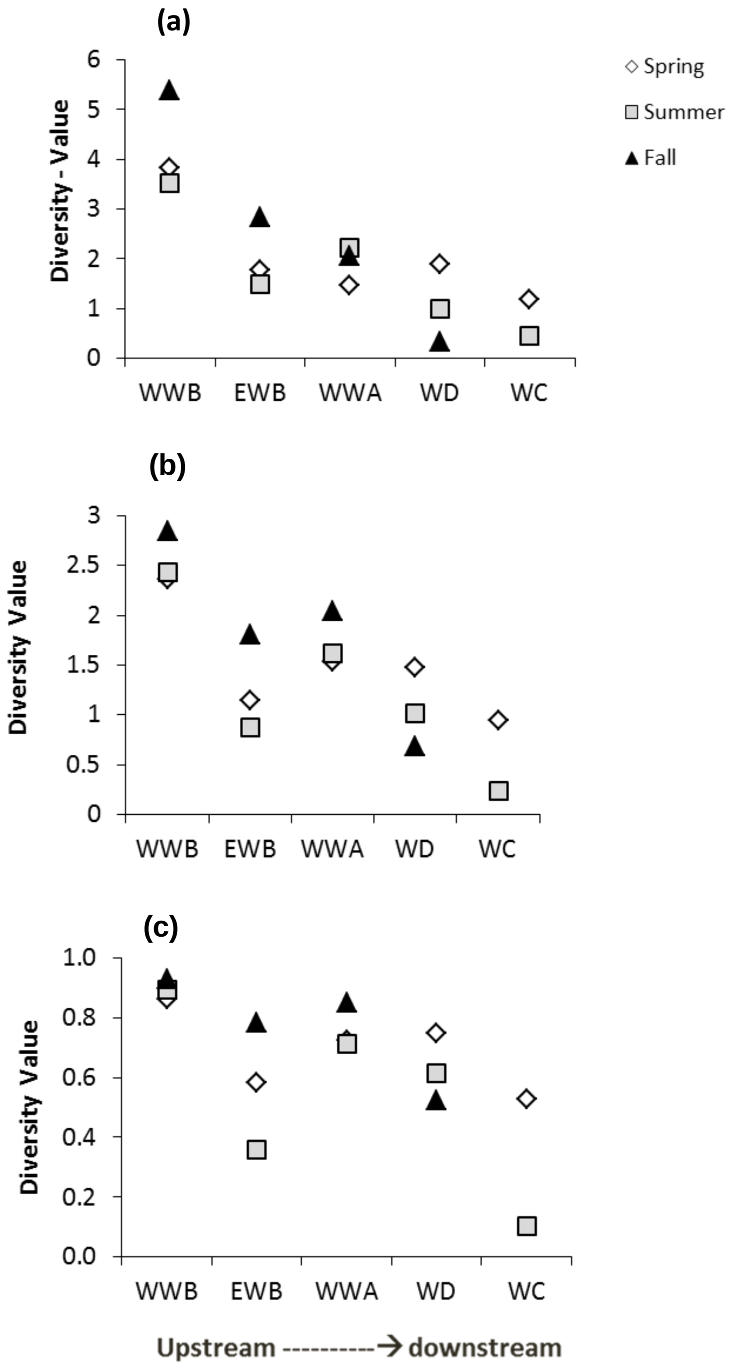

Figure 3.3 Diversity-Indices of benthic macroinvertebrate composition for spring, summer and fall along the Walker River from lowest elevation to highest elevation sites (WC) to highest elevation sites (WWB). (a) Margalef's Diversity Index, (b) Shannon-Wiener Index, (c) Pielou Evenness Index.

The increase in the HBI indexindicated a BMI community shift from pollutant-intolerant taxa (lower HIB index) at the upstream sites to pollutant-tolerant taxa (high HIB index) at the downstream sites (Figure 3.4 a). Mean HBI values among sites range from 3.0 (WWB) to 4.6 (WC). Species composition with high tolerance values at downstream sites belonged to *Baetidae* and *Caenidae* (*Baetis tricuadatus*, *Callibaetis*, *Caenis*, *Fallceon*, *Centroptilum*), where BMI composition switched to species with low tolerance values at upstream sites (Plecoptera and Ephemeroptera).

HBI values were relatively consistent between reaches, except for site WWB, which had significantly lower HIB values (ANOVA, p = 0.013, Figure 3.4 b). The variability among seasons indicates that species distribution can change temporally within same sites. The largest variation was found at site WWA (range: 3.1 in spring to 4.3 in summer and fall) and the least variation was found at site EWB (range: 4.3 in spring and fall to 4.8 in summer.

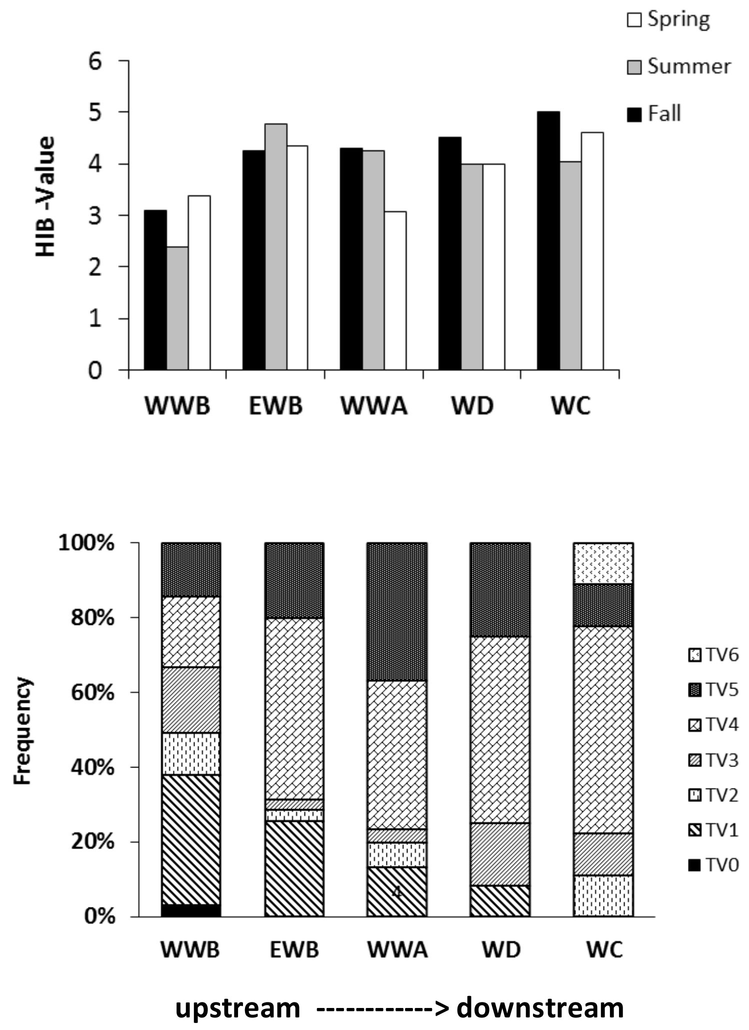

Figure 3.4Seasonal variation in the Hilsenhoff Biotic Index (HIB) values (a) and frequency of tolerance values (TV)(b) for BMI communities collected from five sampling sites along the Walker River from upstream to downstream locations.

The percentage of BMI species with very low TV (0 and 1) in the community composition increased from 10% (site WD) to 40% (site WWB) whereas species with higher TV (3 to 5) were found in varying proportions at all sites (Figure 3.4b). Species with the highest TV of 6 sampled in this study was only found at site WC.

3.3.3 Benthic Macroinvertebrate Biomass

A total of 907 animals belonging to 37 taxa were collectedfor biomass estimation. In Figure 4 the total number of species (a), total densities (b) and total biomass (c) of all animals during spring, summer and fall shown. Sites EWB and WD were not sampled during fall. The number of taxa differed spatially and temporally and decreased with distance from headwaters from 21 taxa at WWB (46 km from headwaters) to 3 taxa at WC (131 km from headwaters).

Estimated densities of BMI were highest at sites EWB and WWB (378 and 381 animals per m^{-2}, respectively) throughout the sampling and lowest at downstream sites WD and WC (48 and 187 animals per m^2, respectively) (Figure 3.5 a). The total BMI biomass at each site was highest in spring and decreased during summer and fall (Figure 3.5b). The total biomass was highest in spring at each site: WWB in spring (587 mg/m^2), WWA (240 mg/m^2), EWB (299 mg/m^2), WC (63 mg/m^2), WD (21 mg/m^2), and lowest in fall: WWB (32 mg/m^2), WWA (26 mg/m^2), and WC (1 mg/m^2). Downstream sites WC and WD presented a higher density to biomass ratio in spring indicating the predominance of smaller body size of benthic invertebrates relative to the upstream sites WWA, EWB and WWB (Figure 3.5c). BMI density and total BMI biomass were positively correlated with Shannon-Wiener-Index in spring (Figure 3.5 a-c). However, trends were less clear in summer and fall; particularly density and biomass seem to be less affected by substrate size.

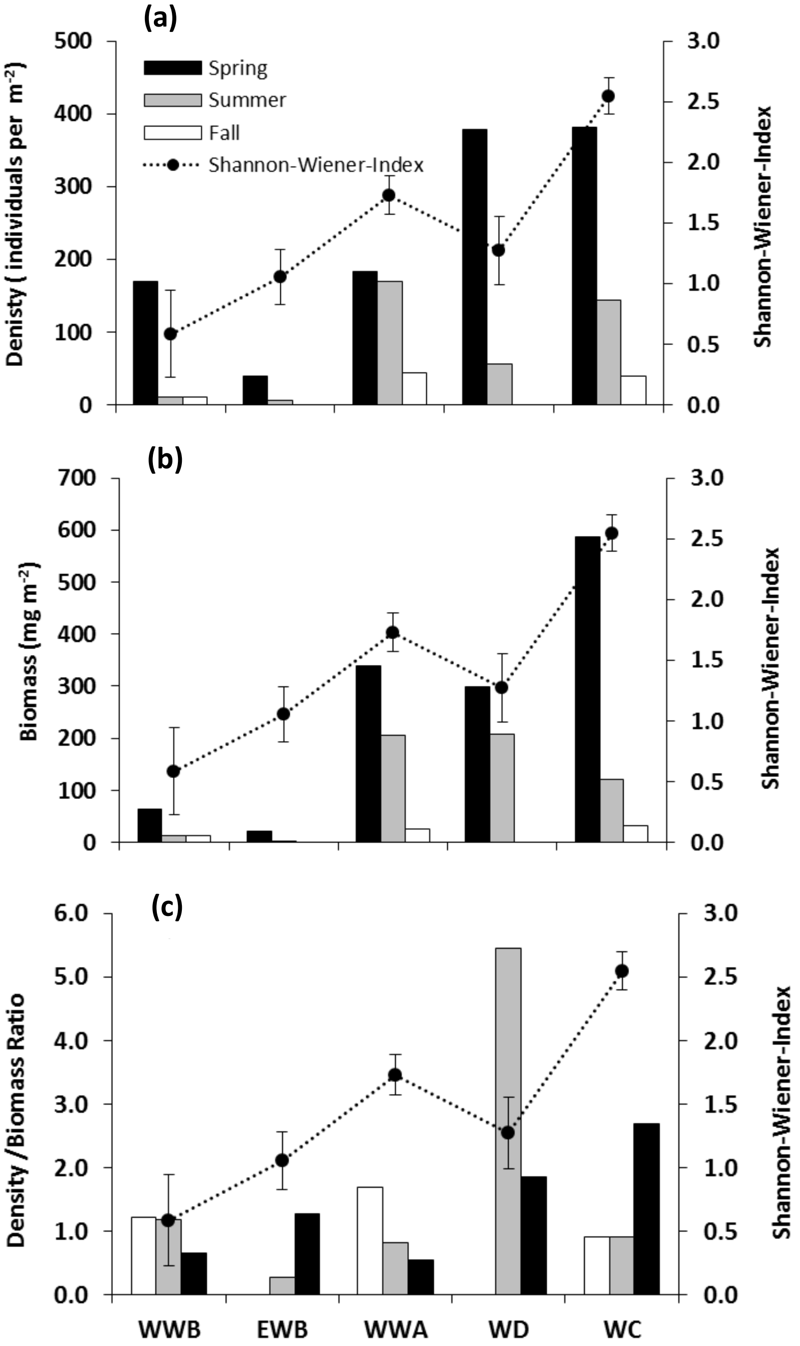

Figure 3.5 Benthic macroinvertebrate density (a), biomass (b), and density to biomass ratio (c) for five sampling sites along the Walker River from upstream, to downstream locations. Benthic macroinvertebrate density and benthic macroinvertebrate biomass include all benthic invertebrate species collected in spring (black bars), summer (grey bars), and winter (open bars). Dashed line represents the Shannon-WienerIndex.

3.3.4 Effect of Habitat Characteristic on BMI Diversity and Biomass

The number of individual organismsin the Walker River was positively related to stream width ($r^2 = 0.639$, $p < 0.01$, Table 3.3), and substrate ($r^2 = 0.527$, $p<0.05$) and negatively related to TSS ($r^2 = -0.605$, $p < 0.05$). Diversity indices were negatively related to temperature (Shannon-Wiener: $r^2 = -0.530$, $p < 0.05$; Margalef: $r^2 = -0.531$, $p < 0.05$); Pileou: $r^2 = -0.513$, $p < 0.05$). Chemical water quality parameters were negatively related to diversity indices. Particularly, Shannon-Wiener was negatively related to TP, SRP and DIN, indicating a decrease in biodiversity at nutrient-enriched sampling sites. Substrate site was positively related to all diversity indices. The Hilsenhoff index was positively related to SRP ($r^2 = 0.592$, $p < 0.05$), indicating a shift in the BMI community composition to pollutant-tolerant taxa at nutrient-enriched sampling sites. Biomass was positively related to stream width ($r^2 = 0.711$, $p < 0.01$). Biomass seemed also be positively related to substrate size, however the correlation was only marginally significant ($r^2 = 0.503$, $p = 0.08$).

Table 3.3 Spearman's rank correlations between benthic macroinvertebrates densities, diversity indices, biomass and habitat characteristics for the five sites (WC, WD, WWA, EWB, WWB) throughout the sampling season (April, August, September 2010). *$p < 0.05$; **$p < 0.001$.

	Stream Width	Temperature	Substrate	TP	SRP	DIN	TSS
Number Individuals	**0.639****	-0.070	**0.527***	-0.102	0.023	0.084	**-0.605***
Shannon-Wiener	**0.547***	**-0.531***	**0.753***	**-0.520**	**-0.897****	**-0.522***	-0.064
Hilsenhoff	-0.069	0.401	-0.308	0.380	**0.592***	0.460	-0.087
Margalef	**0.741***	**-0.531***	**0.829****	-0.438	**-0.775****	-0.411	-0.206
Pielou	0.310	**-0.513***	**0.495***	-0.248	**-0.667***	-0.450	0.103
Biomass	**0.711****	-0.406	0.503	0.035	-0.406	0.06	0.059

3.3.5 Baetis Densities, Biomass and Production

The genus *Baetis* accounted for about one-third of total biomass at study sites along Walker River. Density and biomass varied spatially and temporally among sampling sites and seasons (Figure 3.6a and 3.6b). Except at site WWB *Baetis*biomass decreased substantially at all sites over the sampling season. Highest *Baetis* biomass was found at sites EWB and WWA in spring (end of April and beginning of May). Densities seemed to be positively related to biomass. Interestingly, at site WWA the high biomass seemed to be caused by less but larger individuals. Density over biomass ratios increased over the sampling season, indicating the predominance of smaller body-size individuals later in the year (Figure 3.6c).

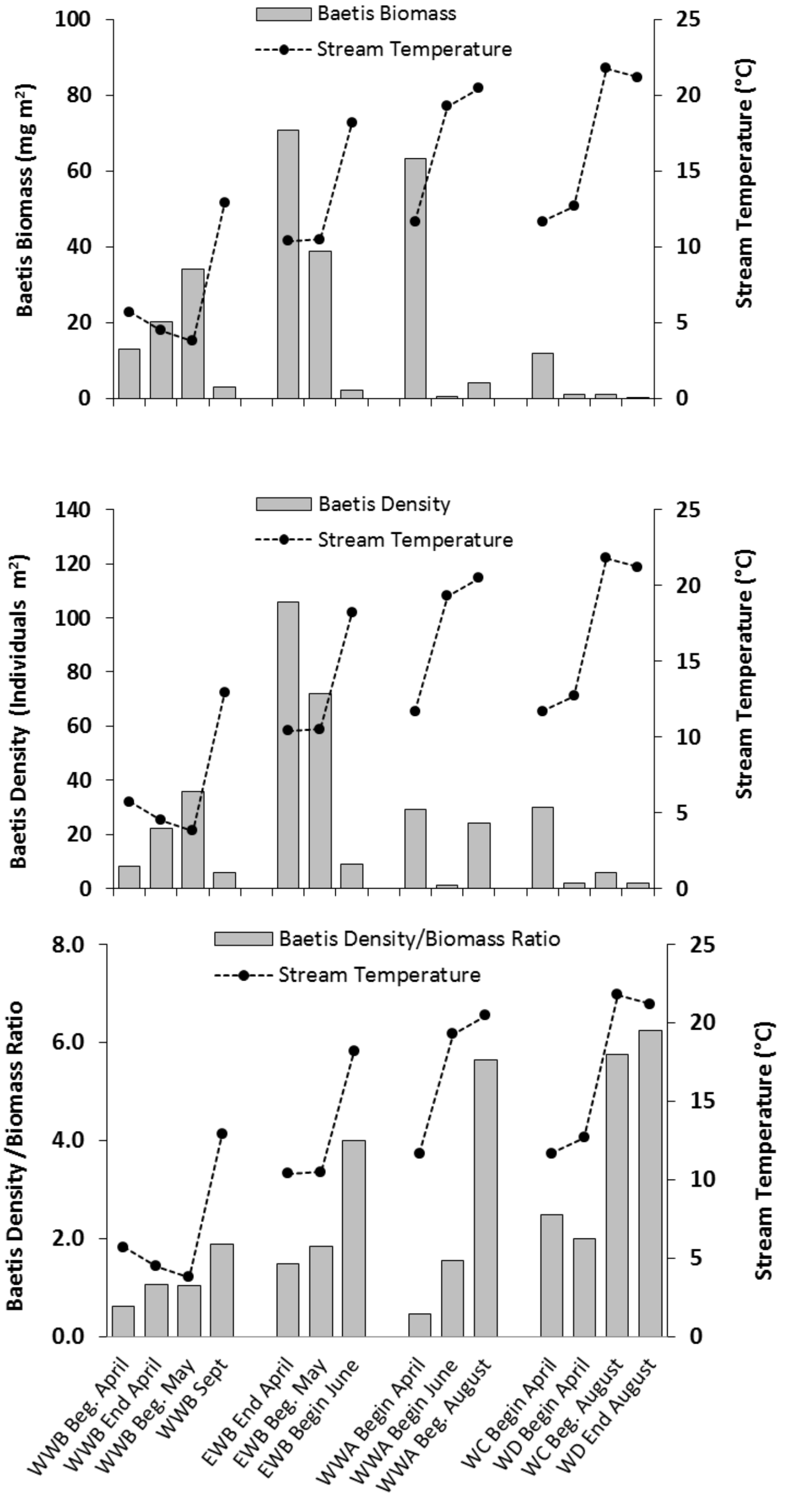

Figure 3.6 Total *Baetis* biomass (a), density (b) and density to biomass ratio (c) for five sites in Walker River, 2010. Dotted line represents stream temperature. Samples from site WC and WD were presented together because these sites were not sampled in fall.

3.3.5Production of *Baetis*Populations between Nutrient-Rich and Nutrient-Poor Sites

Density of *Baetis* was more than two-fold higher at site EWB (270 individuals per m^2) compared to site WWB (124 individual per m^2). Body length was not significantly different between both sites (ANOVA, $p > 0.05$). However, mean body mass at site EWB was significantly lower compared to site WWB (0.77 vs. 0.98 mg, ANOVA, $p = 0.013$), which is the reason for the small spatial variation inmass-length relationships among *Baetis* spp. population among the two sites (Figure 3.7).

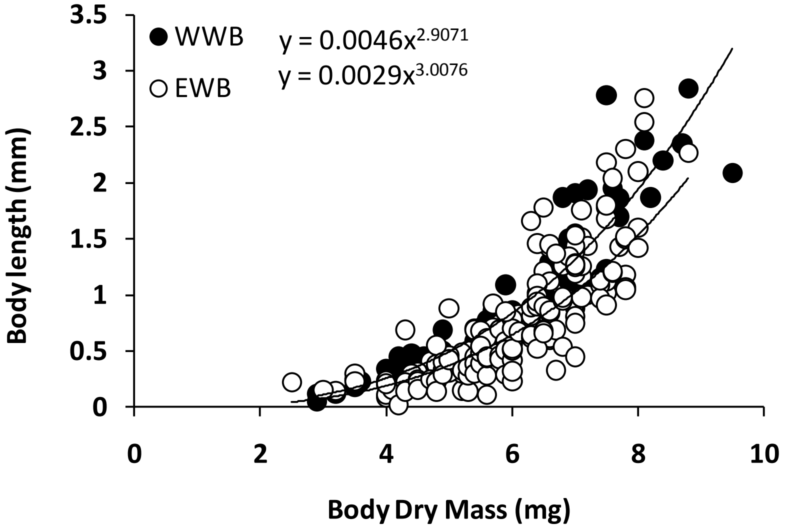

Figure 3.7 Length-mass relationships between *Baetis* from site EWB (open circles) and site WWB (black circles). Also given is the equation for each site.

*Baetis*production for the study period was twice as high at site EWB (1.3 g/m^2) compared to site WWB (0.7 g/m^2, Table 3.4). Further *Baetis* biomass was almost twice as high at site EWB (0.21 g/m^2) compared to site WWB (0.13 g/m^2). Similarly, production at site EWB (1.3 g/m^2) was higher than at site WWB (0.7 g/m^2). The ratio of density to biomass at site EWB was higher (1.29) compared to site WWB (0.95) indicating that at site EWB higher biomass was caused by individuals with smaller body size.

Table 3.4Results of biomass (B), annual production (P), and annual P/Bfor Walker River *Baetis*populations for the sampling period (April to Sept. 2010) at sites WWB (a) and EWB (b).

Size Class	Nr. Baetis in this size class	Density (g m^{-2})	Average Mass (g)	Loss in Density (g m^{-2})	Biomass (g m^{-2})	Loss in Mass (g)	Biomass loss (g m^{-2})	Cohort P (g m^{-2} yr^{-1})
3-4	6	11.1	0.0002	-22.22	0.002	0.0003	-0.007	-0.040
4-5	18	33.3	0.0004	14.81	0.013	0.0006	0.008	0.049
5-6	10	18.5	0.0007	-11.11	0.013	0.0009	-0.010	-0.060
6-7	16	29.6	0.0011	0.00	0.033	0.0014	0.000	0.000
7-8	16	29.6	0.0016	18.52	0.047	0.0023	0.042	0.250
> 8	6	11.1	0.0029	11.11	0.032	0.0022	0.024	0.147
				Biomass (B)	0.14		Cohort	
				Cohort P/B Ratio	2.5		Production (P)	0.35
				Annual P/B ratio	6.0		Annual P	0.84

(b)

Size Class	Nr. Baetis in this size class	Density (g m^{-2})	Average Mass (g)	Loss in Density (g m^{-2})	Biomass (g m^{-2})	Loss in Mass (g)	Biomass loss (g m^{-2})	Cohort P (g m^{-2} yr^{-1})
3-4	5	9.26	0.0002	-44.44	0.002	0.0002	-0.0104	-0.0627
4-5	29	53.70	0.0003	-61.11	0.014	0.0004	-0.0232	-0.1393
5-6	62	114.81	0.0005	38.89	0.057	0.0007	0.0272	0.1633
6-7	41	75.93	0.0009	3.70	0.068	0.0011	0.0041	0.0244
7-8	39	72.22	0.0013	61.11	0.094	0.0017	0.1039	0.6233
> 8	6	11.11	0.0021	7.41	0.023	0.0011	0.0078	0.0467
				Biomass	0.26		Cohort	
				Cohort P/B Ratio	2.66		Production (P)	0.66
				Annual P/B ratio	6.46		Annual P	1.60

3.4Discussion

3.4.1 Benthic Macroinvertebrate Diversity and Biomass along Walker River

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). In this study biotic indices showed tolerance values for the community were highest downstream and generally decreased along an elevation gradient toward the Sierra Nevada. The change of communities in this study of those associated with cooler temperatures, higher discharge, larger substrates, and lower nutrient concentrations (low tolerance values) to those with higher tolerance values at downstream sites was in accordance with other studies (Grubaugh et al., 1996).

Mean HBI index for Walker River communities increased from 3.0 at upstream site WWB to 4.6 at downstream site WC. According to Hilsenhoff (1987) values indicating excellent water quality at upstream site WWB and good to fair water quality at downstream site WC. These values can be associated with increasing anthropogenic disturbance downstream since DIN and SRP increased downstream. However, this tolerance gradient may also have been influenced naturally by a covariate trend in elevation and water temperature and not exclusively by anthropogenic changes. To generate biotic indices to measure present and future conditions of a stream or stream reach, reference data sets are required (Karr, 1981). Assigning indices requires 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. The difficulty of establishing accurate tolerance values is a common problem in arid, mountainous, and poorly studied regions of western North America (Blinn andRuiter, 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 (Sada, pers. comm.).

Water temperature also increased downstream and it cannot be excluded that species in this study with higher tolerance values for organic pollution (e.g. *Baetis tricaudatus*, *Callibaetis*, *Fallceon*) also have higher tolerance values for changes in temperature. Therefore, the utility of this information to understanding community-environment relationships in context of human and natural influences on the river environment are limited (e.g. Poff, 1997;Ciesielka and Bailey, 2007). 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 andStrand, 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 (Poff, 1997).

Substrate size has long been recognized to be one of the most important habitat characteristics to affect BMI distribution (Culp et al., 1983; Erman and Erman, 1984; Kaller and Hartman, 2004). BMI biomass and density were positively related to substrate size along Walker River. This is in line with other studies how reported an increase in *Baetis* biomass in an Appalachian stream was attributed to larger and more physically stable substrate (Wallace and Gurtz, 1985) and total density of BMI from east Canadian streams were higher on gravel compared to sand (Bourass and Morin, 1995). Reasons for the positive relationship are higher surface areas available for the colonization of invertebrates (Allan, 1995), retention and accumulation of organic matter and creation of microhabitats of reduced hydraulic stress and for foraging (Rempel, 2000). BMI biomass was also highly variable spatially and temporally along the Walker River. The dramatic decrease of biomass and density during summer and fall might be the result of decreased discharge due to water withdrawal for agricultural purposes along Walker River.

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 led to a longitudinal shift in the community gradient below a reservoir in the Blue River, Colorado (Voelz and Ward, 1990). Understanding and predicting community shifts at the watershed level can be extremely valuable for optimizing flow restoration and monitoring these shifts over time can lead to valuable insights and inform an adaptive management program (Lake et al. 2007). These objectives are particularly valuable in the context of the hydrologic restoration goals of the Walker Basin Program. Maintaining a high BMI richness would most likely improve fish populations in the Walker River as it has been shown for oceans were higher invertebrate richness was significantly positive related to fish species (Worm et al., 2006).

3.4.2 Baetis Biomass and Secondary Production

Baetis biomass and densities were highly variable throughout the sampling season along Walker River. However, high spatial and temporal variation of *Baetis* biomass and density might also be explained by the life history. The highest *Baetis* biomass and densities found at site EWB might be explained by several factors, which are not exclusive and difficult to separate. Secondary production of *Baetis*was higher at site EWB compared to site WWB. Several factors can be attributed causing those differences between both study sites. The mean stream temperature at site EWB was > 1.6 fold higher than at site WWB. Further, differences in food quality might have contributed to differences in increase in secondary production between the sites. The mean nitrogen content of periphyton (% per dry mass) - an important food source for the grazer *Baetis* - was almost twice as high at site EWB compared to site WWB (2.52±0.67 vs.1.32±0.52), whereas the phosphorus content (% per dry mass) was slightly higher at site EWB (0.25±0.02 vs. 0.18±0.06). Previous studies showed that larval developmental time was affected by a combination of temperature and diet (Fisher and Grey, 1983; Sweeney et al., 1985).

Higher water temperatures and food quality, particularly during the summer months at site EWB most likely led to higher growth rates of *Baetis*. The lower body size of *Baetis* at site EWB might be the consequence of competition due to higher densities. Hart (1987) showed experimentally that final larval biomass of the grazer *Glossosoma nigior* was significantly negatively related to density suggesting competition for periphyton. Although the body mass of *Baetis* population at site EWB was significantly smaller compared to those at site WWB, higher densities, particularly in the larger size cohorts consequently led to higher biomass and production. Previous studies on midges demonstrated the negative relationship between biomass and growth rates. While in a desert stream, high production of midges larvae were caused by rapid growth rates, short life cycles and smaller adult sizes, in a temperate forest stream the high midge production was attributed to longer life cycles, slower growth and larger adult size (Gray 1981, Berg and Hellenthal 1991). Estimates of *Baetis* secondary production at site WWB was similar compared to results from Rader and Ward (1989) for *Baetis tricaudatus* (0.62 g/m^2yr^{-1}) for an unregulated section of the upper Colorado River. Secondary production estimates from this study were lower than those reported for *Baetis tricaudatus*from two Idaho streams (5.7 and 6.2 g/m^2yr^{-1}). *Baetis* production in this study was higher than those reported from Rocky mountain streams with different Zn levels (see Table 3) (Carlisle and Clements 2003). However, average water temperature – an important factor related to invertebrate growth – at site WWB and EWB was 3-fold and 5-fold higher, respectively compared to the Rocky Mountain streams. Results from both sites were similar of those reported for *Baetis tricaudatus* (1.03 g/m^{2}yr) from a spring-fed stream in east Canada (Dobrin and Giberson, 2003). Fisher and Grey (1983) reported very high annual secondary production of 21.9 g/m^{2}yr) for *Baetis quilleri* in Sycamore Creek, a desert stream in Arizona. The production over biomass ratio is related to growth rate and turnover time (Benke, 1984). The P/B ratio was higher at site EWB (6.46) compared to WWB (5.4), indicating increased productivity and growth at site EWB. Rader and Ward (1989) demonstrated an increase of P/B ratios from in *Baetis tricaudatus* population sampled at regulated sites (impoundments) in the upper Colorado River.

3.5Conclusions

In Walker River BMI diversity, richness and biomass is highly variable temporally and spatially. Changes in water temperature, discharge, substrate size, and nutrient inputs along an elevation gradient seem to be major factors shaping BMI community composition and BMI biomass distribution in the river. High pollutant tolerance species were more abundant at sites collected from downstream reaches, were species assigned to a less tolerance values were more frequent at upstream sites. Differences in secondary production of *Baetis* populations between sampling sites might be attributed in higher mean water temperature and increased food quality due to anthropogenic nutrient inputs. However, if these patterns are caused solely by environmental changes in the stream gradient or by anthropogenic disturbances or a combination of both are still difficult to answer. 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. However, results from this study imply that an increased in discharge and a reduce of water temperature as well as reducing nutrients would improve river conditions and concomitantly beneficially affect aquatic communities and will support management plans according to the implemented restoration of Walker River.

CHAPTER 4

STOICHIOMETRIC RELATIONSHIPS BETWEEN AQUATIC SNAILS AND HABITAT CHARACTERISTICS: A CASE STUDY IN SPRING ECOSYSTEMS OF EASTERN NEVADA

Abstract

Ecological stoichiometric theories explaining consumer-producer relationships in spring ecosystems have received little attention despite being among the most diverse ecosystems in the world. In this study, spring-dwelling snail species and their potential food sources were collected from twenty-three springs along an elevation gradient from the eastern part of Nevada. The aim of this study was to link the elemental composition of snails to taxonomy, food resources and habitat characteristics. The results showed that body %P of snails was highly variable ranging from 0.17% to 1.87% among taxonomic groups whereas %N (3.2 to 12.7%) and %C (24 to 54%) content varied less. Differences in the body elemental composition among same populations collected from multiple springs indicate that aquatic snails can deviate from homeostasis. Lower body %P in snails belonging to *Pyrgulopsis* genus collected from warm springs (water temperature ≥ 20ºC) indicate that temperature is an important habitat variable influencing snails' body stoichiometry. Further, consumer-resource imbalances were significantly higher in warm springs compared to cold springs, which may have further consequences on nutrient recycling among springs differing in water temperature. Although the nutrient content of basal food resource was lower and highly variable among springs, snail elemental composition was less explained by their potential food source. It seems that water

temperature is an important factor that can affect food web dynamic in springs. Similar to organisms from lotic and lentic ecosystems, snails in springs might have developed adaptive strategies to cope with low quality food. Thus, changes in land use due to anthropogenic impacts may be more severe for snails in spring ecosystems compared to benthic organisms in lotic and lentic systems.

4.1 Introduction

Springs have long been recognized as unique ecosystems differing from other aquatic systems by their individual water clarity, extreme ranges in water temperature, physicochemical long-term stability (Odum, 1957; Malanson and Kay, 1980), and complex biotic and trophic interactions (Collins et al., 1976). Particularly desert springs are scientifically important because they are often the only source of water, they are often isolated, and effects of habitat fragmentation after the Pleistocene era on population distribution, population genetics, and species specialization can be observed (Myers and Resh, 2002). Endemism is common in many springs and evolutionary theory predicts that some aquatic organisms may adapt by directional selection to those stable habitats (Taylor, 1985; Williams and Danks, 1991; Erman and Erman, 1995; Ferrington 1995; Williams, 1996; Hershler, 1998; Nekola, 1999; Baldinger et al., 2000; Polhemus and Polhemus, 2002; Zullini et al., 2011). Thus, it can be assumed that spring-dwelling organisms may be different in terms of temperature and pollution tolerance, respectively compared to conspecifics in less stable habitats such as lotic or lentic systems. Because temperature is closely related to metabolism, growth rate, and elemental composition in poikilothermic organisms (Atkinson, 1994; Woods et al., 2003); it can be further assumed that spring organisms are stoichiometrically different among springs and among other freshwater systems.Variability in population size and assemblage structure of aquatic life in persistent springs is low compared to other aquatic systems, and springs are often occupied by animals that cannot occupy highly variable environments (van der Kamp, 1995). These characteristics suggest that processes influencing life in springs are trenchantly different than those affecting lotic ecosystems, and that knowledge of lotic system ecology may have little relevance to spring systems.

Freshwater snails are ubiquitous and inhabit many of the spring-related water bodies scattered throughout the southwestern U.S. (Hershler, 1994;Cantonati et al., 2006;Unmack and Minckley, 2008). It has been recognized that their long-term isolation and disconnection from other water bodies after the Pleistocene era have led to habitat fragmentation and, in turn, to distinct population distributions, population genetics and speciation (Myers and Resh, 2002). Local endemism is common and many snail species are restricted to a single spring, spring complex or drainage system (Hershler, 1984; Hershler, 1998; Hershler, 1999). When springs are persistent, they are generally more stable than lotic and lentic systems because they are not exposed to seasonal variability in water chemistry, temperature and discharge (McCabe, 1998). These characteristics suggest that processes which determine elemental composition of freshwater snails for example, are trenchantly different than those affecting lentic and lotic ecosystems and may have little relevance to spring systems. As shown for lentic and lotic ecosystems, aquatic animals vary in their body elemental composition (Villar-Argaiz et al., 2002) due to differences in phylogeny, trophic status, and body size (Liess and Hillebrandt, 2005;Woodward et al., 2005;Small and Pringle, 2010). Temperature acclimatization can also effect organismal chemical composition. For a broad range of taxonomic groups, poikilothermic organisms exposed to cold temperature had higher N and P content (Atkinson, 1994;Woods et al., 2003). This was mainly attributed to either an increase in contents of catalytic components (i.e. P-rich rRNA and N-rich proteins) or by increase in body size. Because freshwater snails in the southwestern U.S. occur among a wide variety of aquatic habitats (Mladenka andMinshall, 2003;Hershler and Sada, 2002; Sada et al., 2005) we assumed that particular differences in the water temperature may be reflected in their body elemental composition.

Information about effects of habitat characteristics, such as water temperature, quality and quantity of basal food resources on the elemental composition of a wide variety of freshwater snail taxa and springs is still scarce. Studies on freshwater snails have focused mainly on their distribution and habitat requirements (e.g. Melhop, 1996;Hershler, 1999;Sada and Vineyard, 2002), population genetics (Liu et al., 2003), life histories and abundances (Mladenka and Minshall, 2003), and effects of habitat alteration on freshwater population dynamics (Hershler, 1998;Sada and Vineyard, 2002).

The objective of this study was to characterize the carbon (C), nitrogen (N), and phosphorus (P)content in freshwater snail species from spring ecosystems, differing in physical and chemical characteristics in the eastern part of the Great Basin, United States. The aim of this study was to examine if taxonomy, food quality and water temperature explain snail elemental composition. Snails and their potential food sources were collected from warm and cold springs to determine: (i) the individual snail body length and mass for each genus in order to examine allometric-dependent differences in elemental composition; (ii) snail %C, %N, and %P, C:N, C:P and N:P ratios in order to examine temperature-dependent variation in elemental composition, and (iii) the elemental composition of basal food resourcesin order to examine the magnitude of elemental imbalances. Due to long-term isolation of many of these snail populations differences in the elemental composition of same species collected from multiple springs can be expected. Results from this study will contribute to the understanding of food web dynamics in spring ecosystems which have not been considered yet in the field of ecological stoichiometry.

4.2 Material and Methods

4.2.1 Study Area

Twenty-three springs spanning a wide range of chemical and physical characteristics were selected according to the historic occurrence of spring-dwelling snails. Springs were located within the eastern part of Carbonate-Rock-Province in Clark, Nye, and White Pine counties, Nevada (Figure 4.1) which extends from western Utah through central and southern Nevada, and into eastern California (Hershey et al., 2007). Paleozoic carbonate rocks, the dominant geologic unit, are exposed in the mountains and underlie many of the valleys (Dettinger, 1989). These fractured carbonate rocks form aquifers in a regional groundwater flow system that receives water from high altitude recharge areas (Welborn andMoreo, 2007). Cenozoic sand and gravel deposits of the overlying basin-fill aquifer yield water readily to springs and wells and are the major water supply for agriculture, livestock and municipal use (Harrill and Prudic, 1998;Welch et al., 2008). Groundwater quality in this region is characterized by low dissolved oxygen and nitrate concentration (2.5 and < 1 mg/L, respectively), and a high total dissolved solids concentration (~ 410 mg/L) (Berndt et al., 2005). The climate in this region is typical of the high desert with temperatures ranging from -11 to -2°C in winter and 18 to 27°C in summer. Annual precipitation varies greatly between valley locations ranging from 20 to 38 cm annually, as snow in the winter and as rain in the summer (Hershey et al., 2007).

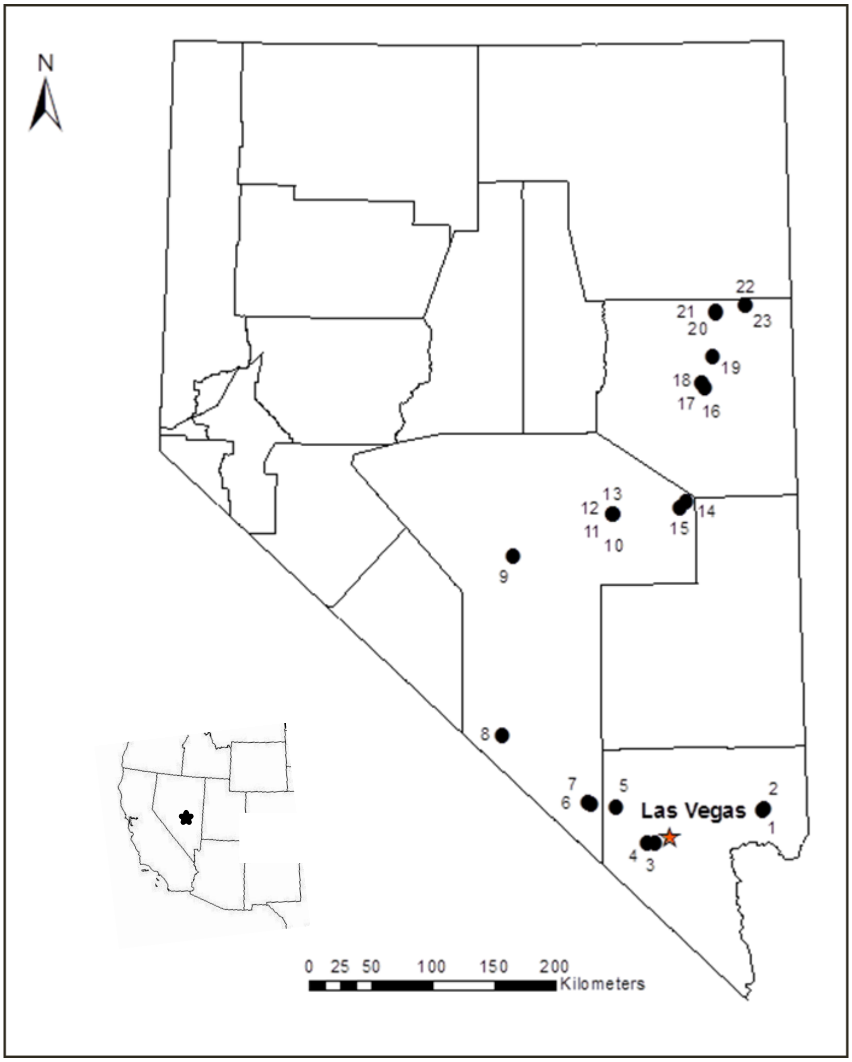

Figure 4.1 Locations of the twenty-three spring sites in Nevada sampled in May 2012.

The majority of the large springs occur within the intermonate basins of the carbonate rock province. Thermal groundwater and geothermal resource areas are common in the low-permeability rock province and water temperatures of warm springs in this area are typically 5 to 15ºC above the mean annual air temperature. In south-central and southern Nevada, springs are widely separated by extensive areas with little or no evidence of groundwater discharge. The springs have nearly constant discharge and probably represent points or zones of principal discharge from large regional flow systems.

4.2.2 Sampling and Analyses

Habitat Characterization and Water Quality Sampling

Physical habitat characteristics were sampled along a transect spanning the wetted width of each spring. Electrical conductance, pH, and water temperature were measured once using YSI® or similar meters. Warm springs were discriminated from cold springs according to the US NOAA Geophysical Data Center (1980), when the water temperature was ≥ 20°C (68°F). Velocity was measured using a top-setting wading rod and a Marsh-McBirney Model 2000 flow meter. Discharge was estimated depending on the spring size either by filling a bucket within a certain amount of time or as the product of depth, width and water velocity in five cross sections. Substrate composition was assessed by separating substrate in each of the seven size classes: bedrock, boulder, cobble, gravel, sand, fine, and muck substrate. Each substrate size was estimated visually as the percentage covered of a sampled area of 0.09 m^2 along the transect. Emergent and riparian bank cover was estimated visually as the percentage shaded area over the sampling area. Water samples for nutrient analyses were collected directly at or below the spring source in 1L, acid-washed plastic bottles.

Biological Sampling

Snails were found grazing on periphyton-covered rocks on filamentous algae and water cress. In some springs snails were also collected from fine substrate on the bottom of the spring. Assuming that snails were feeding at the same source where there were collected from, periphyton, filamentous algae, water cress, and particular organic matter (POM) were sampled for stoichiometric analyses. Periphyton was scraped from submerged rocks, filamentous algae and water cress were collected by hand and POM was collected from the bottom using a dip net. Snails were sorted and identified to the genus and when possible to the genus level. Periphyton for chlorophyllα (chl α) measurement was scratched from rocks and 5-45mL of the slurry were filtered through 0.7µm filter. Filters were wrapped in aluminum foil and stored in the dark until analysis.

4.2.3 Nutrient Analyses

Snails and basal food resources were dried at 50°C for 72 h.After drying, individual snails were weighed yielding dry mass (DM) in grams, and each shell length (distance between the tip of the apex and the edge of the bottom lip) was measured with a digital caliper to the nearest 0.01 mm. Body tissues were separated from shells in all snails. Basal food resources and snail tissues were ground to a fine powder. At least 200 µg was used for elemental determination in the analysis. Small animals were pooled (30-40 organisms) to achieve the necessary mass when necessary. Larger snails (*Melanoides tuberculata*) were analyzed separately, and C, N and P analyses were done on the same organisms. Snails and basal food resources were analyzed for P using the ascorbic acid method by digesting samples in potassium persulfate and sulfuric acid for 1 h at 121°C, and P concentration was determined with a spectrophotometer (UV PharmaSpec-1700, UV-VIS spectrophotometer, Shimadzu, Columbia, MD, USA). Apple leaves were used as a standard reference (1515 Apple Leaves, National Institute of Standards and Technology, US Department of Commerce).

Snails and the four basal food resources were analyzed for C and N by dry combustion at 960°C using an elemental analyzer (Perkin-Elmer 2400 Series II CHNS/O Analyzer, Waltham, MA, USA) at Goldwater Environmental Laboratory, Arizona State University. Carbon, N, and P concentrations were calculated as percentage per dry mass (DM), and C:N, C:P, and N:P ratios were calculated based on molar units. Chlorophyll α (mg/L)was analyzed using a spectrophotometer after submerging the filters in 90% acetone for 24 hours. Water samples were analyzed for TP, standard soluble phosphorus (SRP), and TN (nitrite, nitrate, and ammonia-N) at the Water Analysis Laboratory at the Desert Research Institute (Reno) according to APHA (1992) standards.

4.2.4 Statistical Analysis

Spearman rank correlation was used to determine the relative contribution of various predictive factors (environmental variables, to the elemental composition of snails. One-way ANOVA was used to compare differences in % C, %N, % P, C:N, C:P, and N:P across genera. Environmental variables were log-transformed to avoid heterodescedasticity. Further one-way ANOVA or Wilcoxon-test (depending on normal distribution of data sets) was used to test for differences in %C, %N, % P, C:N, C:P, and N:P across same populations found in multiple springs. Spearman's rank correlation was used to explain differences in body elemental composition when same species were sampled from multiple springs. To elucidate temperature as an effect on the elemental composition of same snail populations found in multiple springs, ANCOVA was used where taxonomy (here Pyrgulopsis genera) was the treatment variable (species-effect) and temperature and body size were the covariates. All statistical analyses were done in JMP10.

4.3 Results

4.3.1 Physical and Chemical Characteristics among Springs

The twenty-three springs sampled ranged widely in their physical and chemical characteristics (Table 4.1). Almost all springs showed some kind of alterations, mostly by livestock (seventeen out of twenty-three), recreation (ten out of twenty-three), diversions and dredging (six out of twenty-three). Depending on the TP concentration (O.E.C.D 1982), the trophic status of the springs ranged from ultra-oligotrophic (3 µg/L) to hyper-eutrophic (234 µg/L). NO_3-N and NH_3-N ranged from 4 µg/L to 1770 µg/Land from smaller 2 µg/L to 96 µg/L, respectively. Elevation ranged from 469 (Rogers) to 2002 m (Flat A). Water temperature ranged from 10.9 (Cold Springs) to 36.2ºC (Reynolds East, Reynolds West, Moorman). Conductivity was highly variables among springs, ranging from 270 (Sidehill) to 3660 µS/cm(Blue Point) and the pH was close to neutral (7.2 to 8). Dominant substrate in most of the springs was fine substrate, followed by sand and gravel. Vegetated bank cover was higher than 90% in the majority of the springs and emergent macrophytes cover ranged from 5 (Blue Point, Calico, and Rogers) to 100% (Flat A and Sidehill). Most common basal resources were comprised of periphyton, filamentous algae, detritus, and water cress.

Table 4.1 List of springs sampled in May and June 2012. Site codes, spring type, temperature elevation and trophic status for each spring are provided. Snail community separated by genus and family are shown for each spring.

Spring Name	Site Code	Spring Type	Sampling Date month/year	Temperature °C	Elevation m	Trophic Status *	Snail Taxonomy	
							Species	Family
Rogers	1	Rheocrene/altered pond	May-12	20.9	469	ultra-oligotrophic	Melanoides tuberculata	Thiaridae
Blue Point	2	Rheocrence	May-12	30.0	549	ultra-oligotrophic	Melanoides tuberculata Tryonia porrecta	Thiaridae Cochliopidae
Calico	3	Rheocrene	May-12	24.0	1195	oligotrophic	Physa sp.	Physidae
Lost	4	Rheocrene	May-12	15.2	1366	mesotrophic	Pyrgulopsis turbatrix	Hydrobiidae
Willow Source	5	Rheocrene	May-12	11.2	1768	mesotrophic	Pyrgulopsis turbatrix	Hydrobiidae
Horseshoe	6	Rheocrene	May-12	18.5	1478	mesotrophic	Pyrgulopsis turbatrix	Hydrobiidae
Grapevine	7	Cave Source	May-12	19.9	1420	oligotrophic	Pyrgulopsis turbatrix	Hydrobiidae
Indian	8	Helocrene	May-12	21.8	1298	eutrophic	Physa sp.	Physidae
Sidehill	9	Cave Source	Jun-12	19.9	1852	mesotrophic	Pyrgulopsis isolata	Hydrobiidae
Reynolds West	10	Limnocrene	Jun-12	36.2	1461	mesotrophic	Pyrgulopsis lockensis	Hydrobiidae
Reynolds East	11	Limnocrene	Jun-12	36.2	1461	eutrophic	Pyrgulopsis lockensis	Hydrobiidae
Hay Corral	12	Limnocrene	Jun-12	34.2	1468	mesotrophic	Pyrgulopsis lockensis	Hydrobiidae
North at Lockes	13	Limnocrene	Jun-12	35.2	1469	ultra-oligotrophic	Pyrgulopsis lockensis	Hydrobiidae
Hardy	14	Rheocrene	Jun-12	13.9	1633	mesotrophic	Pyrgulopsis marcida	Hydrobiidae
Moorman	15	Rheocrene	Jun-12	36.2	1617	ultra-oligotrophic	Pyrgulopsis merriami Melanoides tuberculata Physa sp.	Hydrobiidae Thiaridae Physidae
Bennett	16	Helocrene	Jun-12	14.8	1858	mesotrophic	Juga sp.	Semisulcospiridae
Grass A	17	Helocrene	Jun-12	20.6	1863	mesotrophic	Pyrgulopsis	Hydrobiidae
Grass B	18	Helocrene	Jun-12	19.0	1862	hyper-eutrophic	Pyrgulopsis	Hydrobiidae
Cold Springs	19	Helocrene	Jun-12	10.9	1818	eutrophic	Pyrgulopsis serrata	Hydrobiidae
Unnamed 12-53	20	Helocrene	Jun-12	14.2	1793	eutrophic	Pyrgulopsis serrata	Hydrobiidae
Unnamed 12-54	21	Helocrene	Jun-12	11.9	1793	hyper-eutrophic	Pyrgulopsis serrata	Hydrobiidae
Flat A	22	piped/unknown source	Jun-12	14.4	2002	hyper-eutrophic	Pyrgulopsis gruciglans	Hydrobiidae
Flat B	23	Helocrene	Jun-12	15.2	1999	mesotrophic	Pyrgulopsis gruciglans	Hydrobiidae

* trophic status according to TP concentration (O.E.C.D, 1982)

4.3.2 Interspecific Snail Elemental Composition

The elemental content and elemental ratios of thirteen snail taxa belonging to five families was analyzed. The elemental composition of all snail populations combined exhibited considerable variation in %C, %N, and %P (Figure 4.2). Body %P was highly variable and ranged 11-fold from 0.17 to 1.87%. Body %N varied 4-fold from 3.2 to 12.7%. Body %C was less variable and ranged from 24 to 51%. Coefficients of variation (CV) were consequently much higher in %P (35%) and %N (33%) compared to %C (12%). The high variation in the elemental composition was further reflected in the body C:N, C:P, and N:P ratios (Figure 2). The range in C:N ratio was low ranging from 4.1 to 17.2, whereas the C:P ratios varied 10-fold from 56 to 599 and the N:P ratio ranged > 12-fold from 9 to 112. The CV of C:P (33%) and N:P ratios (47%) were therefore higher compared to the C:N ratio (8%).

Significant differences in %C, %N, and %P were also found among snail genera (Figure 4.3). *Pyrgulopsis* had significantly higher %C (43) compared to *Physa* (36) and Melanoides (39) but not significant different form other genera. *Physa* body %N was significantly lower (7.1) than *Pyrgulopsis* (9.5) *Melanoides* (8.6) and *Juga* (9.7), but not different from *Tryonia* (8.3). *Tryonia* had the lowest %P (0.24%) followed by *Melanoides* (0.54%), *Physa* (0.64%), *Pyrgulopsis* (0.66%), and *Juga* (0.69%). Elemental ratios also differed significantly among snail genera. *Physa* had significantly higher C:N ratio (7.1) compared to the other genera. The very low %P in *Tryonia* consequently led to an exceptionally high C:P ratio (461), followed by Melanoides (198), Pyrgulopsis (191), Physa (149) and Juga (145). Similarly, the N:P ratio was significantly higher in *Tryonia* (84) compared to *Melanoides* (38), *Pyrgulopsis* (37), *Juga* (31), and *Physa* (26).

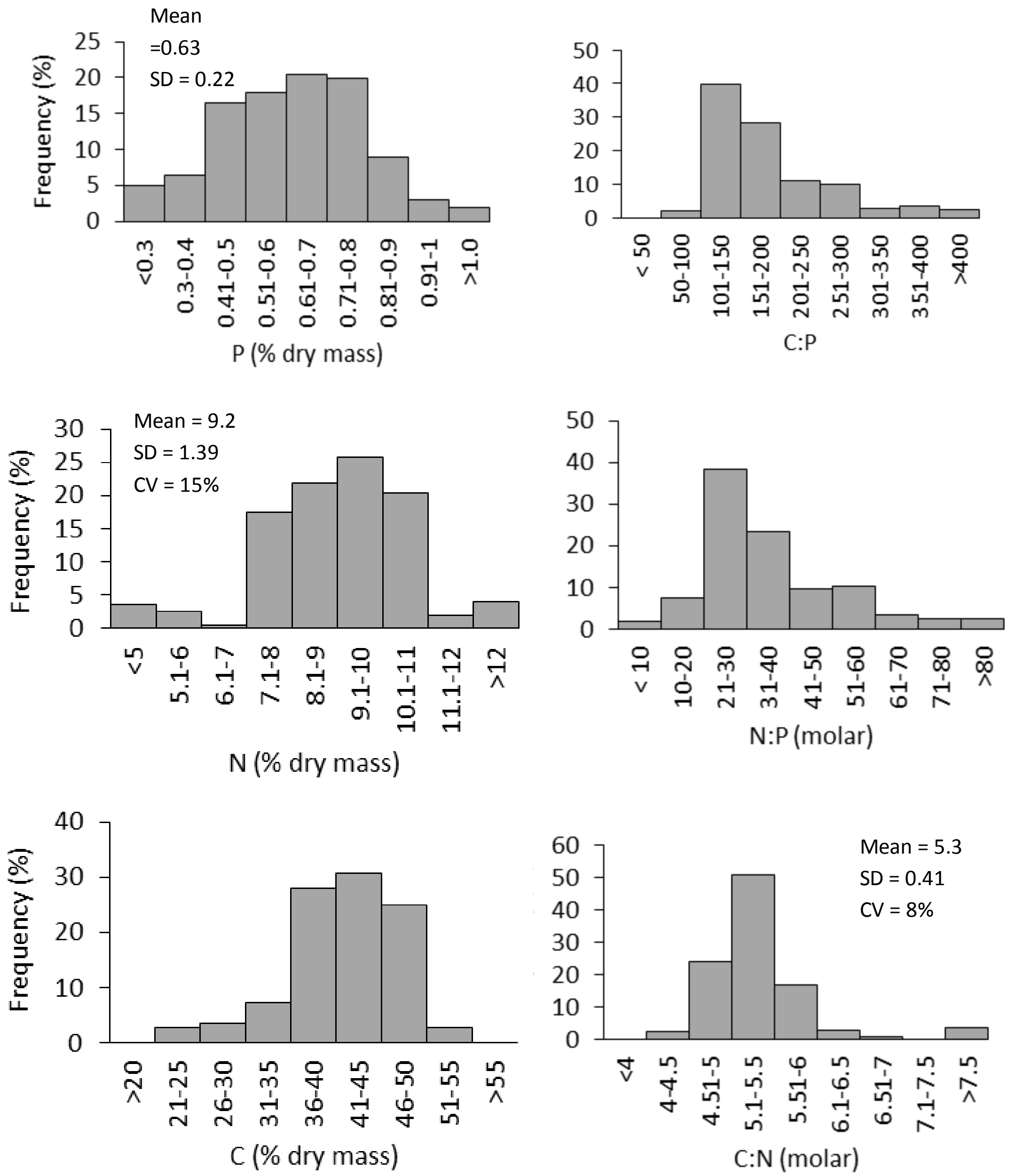

Figure 4.2 Frequency histogram of snail body %C, %N, %P, C:N, C:P, and N:P from all twenty-three springs sampled during May and June 2011.

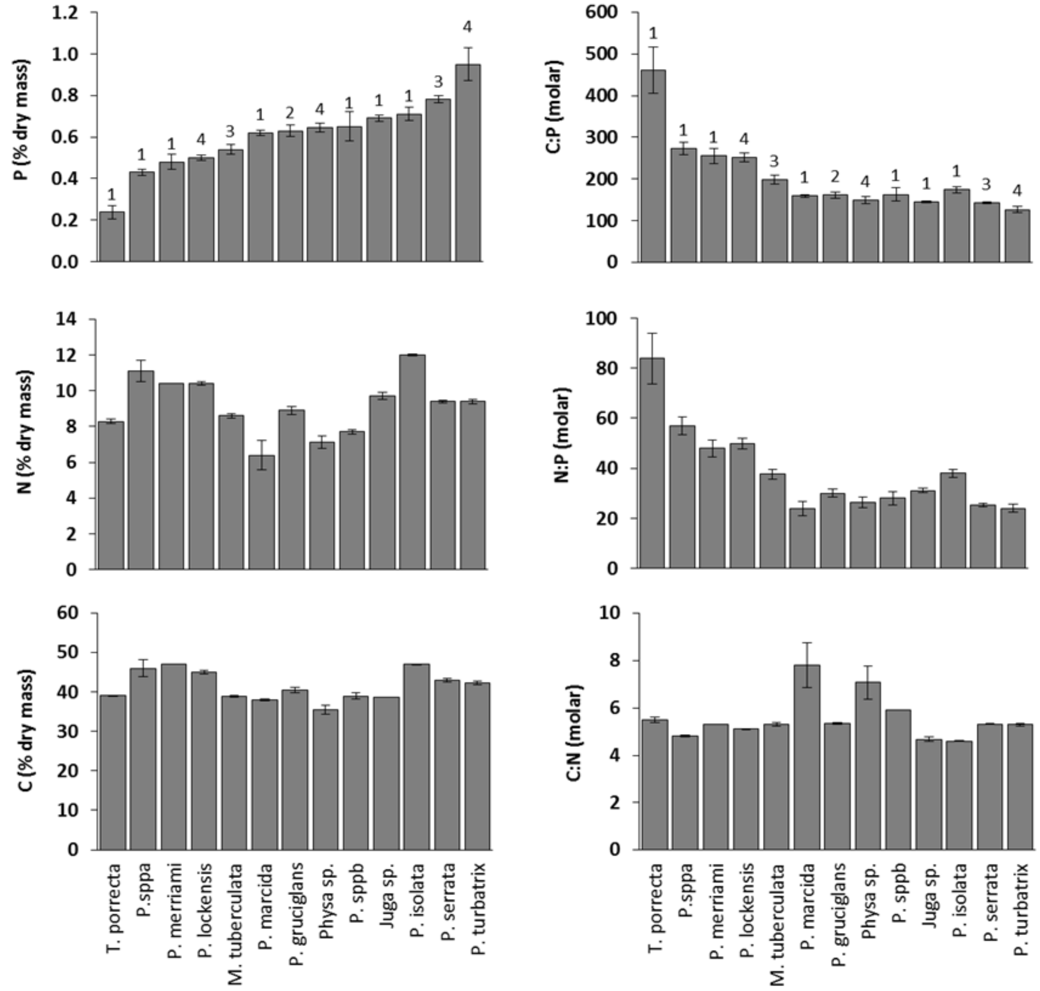

Figure 4.3 Percent body P, %N, %P, C:N, C:P, and N:P ratios (mean± SE) of snail species sampled in 23 springs during May and June 2011. The number of springs each species was sampled is indicated above the error bars.

4.3.3 Environmental Variables and Snail Stoichiometry

Snail body %P was significantly negatively correlated with water temperature (r^2= -0.55, $p < 0.0001$, Table 4.2), whereas snail C:P and N:P ratios were significantly positively correlated with water temperature (C:P: $r^2 = 0.55$, $p < 0.0001$; N:P: $r^2 = 0.51$, p

= 0.009, Table 3). Snail body %P was significantly positive correlated with TP ($r^2 = 0.28$, $p < 0.001$) and negatively related with snail elemental ratios (C:N: $r^2 = -0.25$, $p < 0.01$; C:P: $r^2 = -0.30$, $p <0.001$; N:P: $r^2 =-0.21$, $p = 0.004$). Snail body %P was significantly positively correlated with TP and NO_3-N (TP: $r^2 = 0.28$, $p <0.001$; NO_3-N: $r^2 = 0.25$, $p < 0.001$) and significantly negative correlated to snail C:N, C:P, and N:P (C:N: $r^2=-0.25$, $p = 0.001$; C:P: $r^2 = 0.30$, $p < 0.0001$, N:P: $r^2 = 0.21$, $p = 0.004$). Snail C:P and N:P were further significantly negatively correlated to NO_3-N (C:P: $r^2 = -0.28$, $p < 0.001$; N:P: $r^2 = -0.24$, $p = 0.027$). Snail body %C and %N were weakly but significantly positively correlated with chl α (%C: $r^2 = 0.23$, $p = 0.003$; %N: $r^2 = 0.22$, $p = 0.004$) whereas snail %P had significant negative correlation with chl α ($r^2 = -0.44$, $p < 0.0001$). Consequently snail C:P and N:P ratios had significant positive correlation with chl α (C:P: $r^2 = 0.56$, $p < 0.0001$; $r^2 = 0.49$, $p < 0.0001$).

Table 4.2Spearman’s rank correlation between environmental variables (TP, NO_3-N, elevation, water temperature, chlorophyll-α) and basal food resource stoichiometry (basal C:N, C:P, and N:P), interspecific allometric characteristics (BM = snail body mass), and snail stoichiometry (snail %C, %N, %P, C:N, C:P, N:P). *p < 0.05; **p < 0.001.

	BM	TP	Temp.	NO_3-N	chlα	Basal C:N	Basal C:P	Basal C:P
snail %C	-0.491**	0.039	0.134	-0.037	0.227*	-0.382**	-0.468**	-0.4**
snail %N	-0.361**	0.123	0.145	0.013	0.223*	-0.271*	-0.428**	-0.371**
snail %P	0.126	0.282*	-0.548**	0.249*	-0.44**	0.289*	-0.101	0.284*
snail C:N	0.082	-0.251*	0.129	0.139	-0.075	0.103	0.273*	0.287*
snail C:P	-0.201*	-0.295**	0.506**	-0.284*	0.556**	-0.335**	0.028	0.209*
snail N:P	-0.236*	-0.211*	0.505**	-0.242*	0.491**	-0.322*	-0.026	0.145

4.3.4 Basal Food Resources versus Snail Stoichiometry

Major basal food resources were highly variable and differed significantly in their elemental content and elemental composition (Figure 4.4). Filamentous algae and water cress had higher %N and %P compared to POM and periphyton (N: 3.14 and 3.56 vs. 0.9 and 2.41; P: 0.25 and 0.18 vs. 0.06 and 0.05). Mean %C varied less among the four basal food resources ranging between 20% in POM to 38% in water cress. The C:N, C:P and N:P ratios differed among basal resources. POM had significantly higher C:N than other basal food resources (p = 0.0012). Filamentous algae had significantly lower C:P and N:P ratios than other basal food resources.

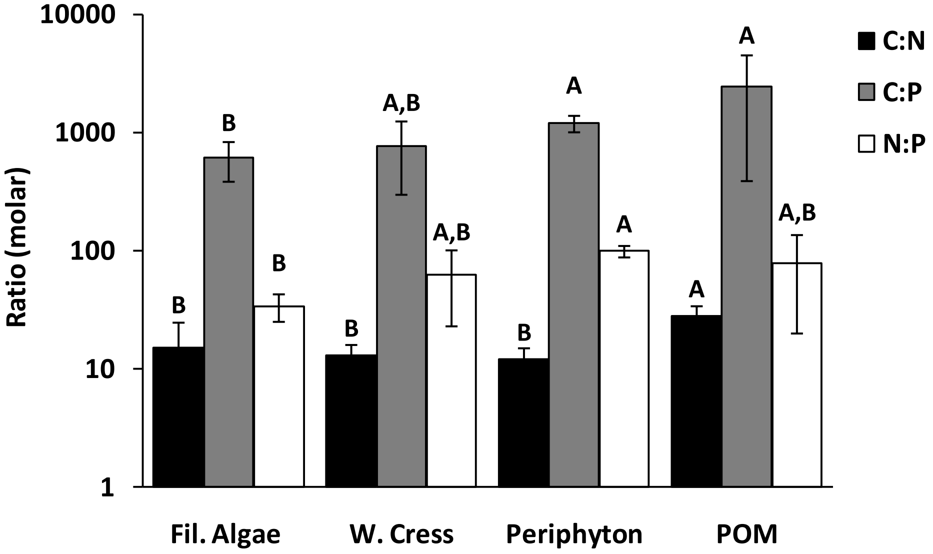

Figure 4.4 Mean C:N, C:P, and N:P ratio (± SD) of filamentous algae (Fil.Algae), water cress (W. Cress), periphyton and particulate organic matter (POM) collected from 23 springs in eastern Nevada between May and June 2012. Different letters indicate significant differences between elemental ratios of major basal food resource determined by Tukey's HSD test. Fil. Algae = Filamentous Algae, W. Cress = Water Cress, POM = Particular Organic Matter.

Snails had significantly higher mean body %N and mean %P than basal food resources (mean N: 9 vs. 3, p < 0.0001; mean P: 0.63 vs. 0.18, p < 0.0001, Figure 4.5a). Consequently, mean C:N and C:P ratios in snails were significantly lower compared to those of basal food resources (mean C:N: 15.2 vs. 15.2, p< 0.0001; C:P: 189 vs. 954, p < 0.0001, Figure 5b). The mean N:P ratio of snails were significantly lower than basal food resources (36 vs. 59, p < 0.0001, Figure 4.5b).

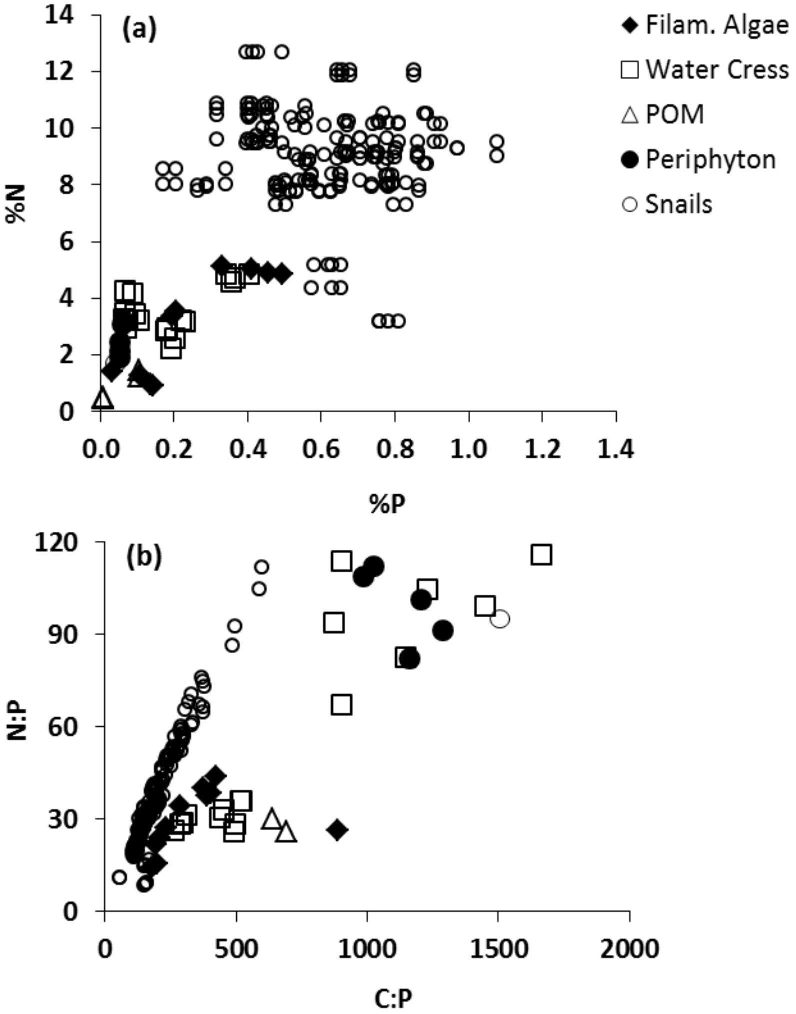

Figure 4.5Individual % N and % P (a) and C:N and C:P ratio (b) of snails and their potential basal food resources combined from the twenty-three study springs.

Elemental imbalances between basal food resources and snail C:N, C:P and N:P were apparent in all springs. However, when springs were separated into warm and cold springs (cold: ≤20 ºC; warm ≥ 20ºC), C:P and N:P imbalances between basal food resources and snails were significantly larger in warm springs compared to cold springs (C:P: 849 vs. 485, $p < 0.0037$; N:P: 43 vs. 25, $p< 0.0001$, Figure 4.6). Elemental C:N imbalances between basal food resources and snails were not significantly different between warm and cold springs(7.7 vs. 8.1, $p = 0.509$).

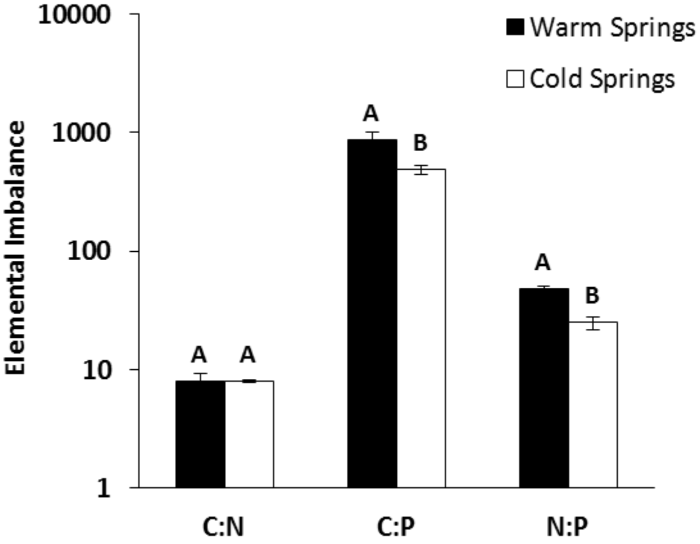

Figure 4.6 Comparison of mean elemental C:N, C:P and N:P imbalance (± SE) between basal food resources and snails from warm (black bars) and cold springs (open bars).

4.3.5 Intraspecific Snail Elemental Composition

Significant differences in the elemental composition among the same populations from multiple springs indicate that most snails do not maintain their body elemental composition (Table 4.3). The body %C in *P. lockensis* sampled from three different springs was not significantly different (p = 0.529).

Table 4.3 Mean (± SE) in body size, %C, %N, %P, C:N, C:P, and N:P of same snail species sampled from multiple springs. Differences between body size, elemental content and elemental ratios were analyzed using one-way ANOVA followed by Tukey-HSD test.

Species	Spring	Body Size	C	N	P	C:N	C:P	N:P
		(mg)		(% dry mass)			(molar)	
P. serrata	Cold Springs	0.97 (0.49)	46 (1.7)	9.8 (0.3)	0.85 (0.1)	5.4 (0)	141 (14.7)	26 (2.68)
	CR12-53	1.14 (0.44)	42 (0.9)	9.1 (0.1)	0.79 (0.1)	5.4 (0.1)	137 (9)	25 (1.59)
	CR12-54	0.82 (0.33)	41 (1)	9.3 (0.4)	0.71 (0.1)	5.1 (0.1)	149 (11.4)	29 (2.43)
	p	0.047	0.001	0.006	0.001	0.001	0.21	0.028
P. gruciglans	Flat A	0.49 (0.13)	38 (0.4)	8.2 (0.2)	0.73 (0.1)	5.5 (0.1)	138 (21.3)	25 (3.9)
	Flat B	0.87 (0.43)	43 (1.7)	9.6 (0.6)	0.60 (0.1)	5.2 (0.1)	185 (21.1)	35 (4.3)
	p	<0.0001	0.001	0.001	0.011	0.000	0.003	0.002
P. lockensis	North @Lockes	0.62 (0.24)	46 (2.9)	10.4 (0.4)	0.49 90.1)	5.1 (0.1)	245 (30.2)	48 (5.4)
	Hay Corral	0.69 (0.16)	43 (6.1)	10.2 (1.7)	0.67 (0.1)	4.9 (0.2)	156 (22.1)	32 (5.3)
	Reynolds West	0.49 (0.22)	46 (0.4)	10.8 (0.1)	0.39 (0.1)	5 (0.1)	305 (44.4)	62 (9)
	Reynolds East	0.55 (0.24)	45 (1.5)	10 (0.4)	0.39 (0.1)	5.3 (0.1)	302 (45)	57 (8.7)
	p	0.049	0.529	0.016	0.012	0.001	<0.0001	<0.0001
P. turbatrix	Horseshoe	1.15 (0.4)	42 (2.1)	9.6 (1)	0.77 (0.14)	5.1 (0.2)	144 (31.6)	28 (6.7)
	Grapevine	0.59 (0.38)	44 (0.3)	9.3 (0.3)	0.87 (0.18)	5.6 (0.1)	136 (29.3)	25 (5.3)
	Willow Source	1.36 (0.4)	41 (0.6)	9.3 (0)	1.22 (0.51)	5.2 (0.1)	100+(34.8)	19 (6.7)
	Lost Creek	0.49 (0.31)	41 (0.1)	10.3 (0)	0.53 (0.12)	4.64 (0.1)	207 (49)	45 (1)
	p	<0.0001	0.025	0.618	0.151	0.002	0.056	0.048
Physa spp.	Calico	n/a	33 (0.40)	7.8 (0)	0.57 (0.1)	5 (0)	153 (13)	30 (2.6)
	Indian	n/a	26 (2.2)	5.2 (0)	0.62 (0)	6.5 (0)	110 (10.20	18 (0.8)
	Moorman	n/a	45 (1.7)	6.7 (3.8)	0.78 (0)	11.1 (6.5)	150 (7.1)	19 (10.6)
	CR 12-53	n/a	37 (0.4)	8 (0)	0.61 (0.2)	5.4 (0)	183 (86.5)	34 (15.9)
	p	n/a	<0.0001	0.118	0.001	0.002	0.002	0.03
M. tuberculata	Blue Point	47.7 (15)	40 (1.6)	8.5 (0.4)	0.56 (0)	5.5 (0)	185 (8.4)	34 (1.8)
	Rogers	192.2 (201)	38 (0.5)	8.3 (0.5)	0.57 (0.2)	5.4 (0.4)	195 (77.2)	36 (13.1)
	Moorman	440.2 (143)	39 (0.2)	9.6 (0.1)	0.45 (0)	4.7 (0)	224 (9.1)	47 (2)
	p	<0.0001	<0.0001	<0.0001	0.002	< 0.0001	0.002	0.032

Significant differences in %N and %P existed among the same populations collected from multiple springs. Only the body %N in *Physa* sp. and body % N in *P. turbatrix* did not vary among the same populations (p = 0.118 and p = 0.618, respectively). Similarly, *Pyrgulopsis serrata* populations sampled from multiple springs showed little variation in C:P ($p = 0.210$). The Chl α content of springs did not explain the body elemental content of snail population. However differences in body size (mg) were significant when same snail populations among multiple springs were compared (Table 4.3).

4.3.6 Effect of Body Mass and Temperature on Snail Stoichiometry

Among all snail species combined body mass was negatively correlated to body %C and %N (%C: $r^2 = -0.49$, $p < 0.0001$; %N: $r^2 = -0.36$, $p < 0.0001$) and positively correlated to C:P and N:P (C:P : $r^2 = -0.20$, $p = 0.014$; $r^2 = -0.24$, $p = 0.004$, Table 4.2). Mean body %P in snails collected from warm springs (> 20°C) was significantly lower compared to that of snails collected from cold springs (< 20° C) (0.57 vs. 0.77, $p < 0.0001$).

The effect of water temperature and body size was also tested among *Pyrgulopsis* species sampled from multiple springs using ANCOVA. Body size was negatively but not significantly related to water temperature. ($r^2 = 0.13$, $p > 0.05$). Body size did not affect *Pyrgulopsis* species elemental content and elemental ratios ($p > 0.05$). In contrast, the same test revealed that snail body % P was significantly different between *Pyrgulopsis* species when this parameter was related to water temperature ($p < 0.0001$, Table 4.2). The snail body %P was significantly negatively correlated with water temperature ($r^2= 0.4$, $p = 0.006$). *Pyrgulopsis* population also differed marginally in their C:P and N:P ratio when both parameter were related to water temperature (C:P: $p = 0.065$, N:P: $p = 0.067$). Further, snail C:P and N:P ratio was positively correlated with water temperature after accounting for species-related differences (C:P: $r^2 = 0.57$, $p = 0.0005$; N:P: $r^2 = 0.57$, $p = 0.0005$).

4.4 Discussion

4.4.1 Taxonomy-Related Snail Elemental Composition

The elemental composition and elemental ratios of freshwater snail genera were assessed in this large scale study to test how taxonomy and habitat variables affect snail stoichiometry. In this study, the elemental content and the elemental composition differed widely among snail genera. Results in Figure4.1) showed that taxonomic identity can be important driver of the elemental composition in our snails. For example, mean body %P ranged > 4 fold, with *Tryonia porrecta* and *Pyrgulopsis turbatrix* having lowest and highest body %P, respectively. Differences in the elemental composition of different species have been attributed to variable proportions of biomolecules, such as ribosomal RNA (rRNA) (Sterner and Elser, 2002). Particularly the body P content in species has been linked to different amounts of rRNA (Elser et al., 2000;Sterner and Elser, 2002).

Differences in snail elemental composition in this study were not appreciably different from mollusk species in other ecosystems, indicating that elemental composition among species belonging to the same animal class is similar. Mean snail body %P in this study was lower than in New Zealand mudsnails (*Potamopyrgus antipodarum*) reared in the laboratory under a high food quality treatment (tissue %P: 0.88, Tibbets et al., 2010), and within the range of snails species found in a Central Poland reservoir (range tissue %P: 0.63 to 1) (Jurkiewicz-Karnkowska, 2002). The C:N, C:P, and N:P ratios of snails collected in this study were slightly higher than those from Indiana and Michigan streams (Evans-White et al., 2005), however snail C:P and N:P ratios from this study were in the range of those from the littoral zone of Lake Erken, Sweden. Snail C:N, C:P, and N:P ratios collected from warm springs were always higher than ratios reported for snails from lotic environments (Evans-White et al., 2005), but were not different from those reported for littoral environments (Liess and Hillebrand, 2005). Snail C:P ratios from the warm springs ($\geq$ 20 °C) were lower than those of the stromatolite-grazing snail *Mexithauma quadripaludium* (C:P: 277) from Rio Mesquites, Cuatro Ciengas, Mexico, an extremely P- limited ecosystem reflected by the very high stromatolite C:P ratio of 2300-2550 (Elser et al., 2005). Thus, it appears that habitat-related variables are more important than the type of the ecosystem in determining snail elemental composition.

4.4.2 Environmental Variables and Snail Stoichiometry

Significant differences in snail elemental composition existed even within same populations sampled from multiple springs. This is in contrast to homeostatic stoichiometric theory, which predicts that the elemental composition of individuals belonging to the same species is relatively constant (Sterner and Elser, 2002). Several hypotheses - which are not necessarily exclusive - We propose that may explain these patterns in springs in this study.

Basal Food Resources and Snail Elemental Composition

Despite a large trophic gradient (TP ranged > 160 fold) and higher ranges in the elemental composition of basal food resources, snail body elemental composition was less variable. Therefore, elemental imbalances, which have been reported from pelagic (Sterner and Elser 2002), lotic (Evans-White et al., 2005) and lentic (Frost et al., 2003) are also likely to apply in crenic habitats. It has been shown that benthic invertebrate deviate from strict homeostasis when exposed to different food quality (Cross et al., 2003;Ferrao-Filho et al., 2007;Small and Pringle, 2010). Although diet appeared to influence elemental ratios in snails in this study (Table 2), a clear trend that higher food quality (lower C:N and C:P) was related with higher snail body %P or %N among same snail populations from springs differing in food quality was not observed.

Basal food resources in the springs we sampled had very low nutrient contents (Figure 4). The C:P ratio of basal food sources from 200 (filamentous algae) to > 4000 (POM) and were higher than those reported in other studies on freshwater snails (e.g. Tibbets et al., 2010, C:P: 1119), (Liess andLange, 2011, CP: 60-600). Tibbets et al. (2010) showed that New Zealand mudsnails (*Potamopyrgus antipodarum*) feeding on algae with high C:P ratios (C:P ratio = 1119) were constrained in growth and adult body size. However, effects of low food quality (high C:P ratios) of basal resources on snails growth was not assessed because data were sampled only once at each spring. It has been experimentally shown, that growth rates of the freshwater snail *Elima livesences* were reduced under the combination of low food quality and quantity without changing its body %P (Stelzer and Lamberti, 2002). However, feeding on basal food resources which are dissimilar with an organism's body elemental requirement does not necessarily mean that an organism faces limitations in growth. Organisms have developed different strategies to cope with low quality food, such as compensatory feeding (Taghon, 1981;Stelzer and Lamberti, 2002). As a response to low quality food, the snail *Elimia livensens* increased consumption of low quality food when fed ad libitum without any limitations in growth (Stelzer and Lamberti, 2002). This strategy might have been adapted by snails which inhabit those springs were food quality was v low however food quantity (Chlα concentration) appeared to be high (e.g. Moorman Springs). Lower food quality in warm springs subsequently led to significantly higher producer-consumer elemental imbalances (Figure 6). The same trend was found by Dobberfuhl and Elser (2000) where seston-zooplankton C:N and C:P imbalances in cold artic lakes were significantly lower than those from temperate lakes.

However, contrary to our findings, zooplankton in cold lakes had higher C to nutrient ratios, which was attributed to a higher lipid content; consequently affected the C content and resulted in higher C:N and C:P ratios (Sargent and Falk-Petersen, 1988). In our study, the water temperatures - even in the cold springs - were likely too high for the snails to develop adaptive strategies, such as an increased lipid content reflected by the relatively constant %C throughout all species and springs (Figure 4.3).Elemental imbalances between snails and their potential basal food resources can have significant implications for nutrient recycling in springs.

Temperature-Related Snail Elemental Composition

Organismal growth rates have been shown to be positively correlated with temperature. According to the growth rate hypothesis, organisms should exhibit higher rRNA which would result in increased %P and lower C:P and N:P ratios (Main et al., 1997;Gillooly et al., 2002;Acharya et al., 2004;Acharya et al., 2006). Results in this study contradict this hypothesis. *Pyrgulopsis* genera body %P was negatively related to water temperature and had higher C:P ratios than conspecifics from the cold springs. Snail populations with the highest body %P - *Pyrgulopsis isolata, Pyrgulopsis serrata* and *Pyrgulopsis turbatrix* - were collected from the cold springs. The exceptionally high body %P of 1.22 in *P. turbatrix* collected from Willow source Spring might therefore be explained by the low water temperature of 11.2 °C because body size did not explain any of the variations in the *Pyrgulopsis* species.

However, temperature can have differential effect on growth and N and P accumulation simultaneously, i.e. similar to snails in the warm springs, higher growth and development rates of snails in the warm springs might dilute nutrient pools (Jonasson et al., 1999;Woods et al., 2003).It seems that temperature has a strong effect on the snail elemental composition and consequently elemental ratios. The magnitude of body % P in snails was negatively related to the water temperature and, the nutrient content in the snail tissue from the cold springs was significant higher than the snails from the warm springs. This result is in line with Woods et al. (2003) who showed that poikilothermic cold-exposed organisms averaged 30 % and 50 % more N and P, respectively, than warm-exposed conspecifics. This difference has been attributed to temperature-related effects on biochemical mechanisms (Kanda et al., 1994;Pinedo et al., 2000), and on evolutionary and adaptive effects such as altering rates of N and P uptake and loss or dilution of nutrient pools due to temperature-related growth rates (Jonasson et al., 1999;Woods et al., 2003). Another reason for a higher nutrient content in cold-acclimated organisms was attributed to extensive internal reorganization, including larger cell size or body size (Wood et al., 2003; Atkinson, 1994). The ‘temperature-size rule’ (Atkinson, 1995; Atkinson, 1996; Walters and Hassall, 2006) predicts a larger body size of poikilotermic organisms at maturity in cold environments where growth efficiency decreases with increasing temperature.

However, same populations were only found in three or four springs with high and low temperatures and the sample size was too small to fully support this model. Contradictory to the temperature-size rule and by using the Bertalanffy-Perrin model (von Bertalanffy, 1960;Perrin, 1995), Angilletta and Dunham (2003) showed that growth efficiency in most poikilothermic organisms, including mollusks, was somewhat positively related or insensitive to temperature. Thus, proximate mechanisms between body size and temperature were much more complex even in closely related organisms (Angilletta and Dunham, 2003).

Additionally, the negative relationship between body size and temperature in our springs might simply be caused due to a lower adult-to-juvenile size ratio, i.e. a higher proportion of small juveniles in cold springs at the time of the sampling. Unfortunately, insufficient data are available regarding hatching and final snail sizes for our study snails and it would have been difficult to accurately separate juveniles and adults by using a fixed shell length. Woods et al. (2003) concluded that organisms may respond to differences in temperature not only by increasing size, but also by changes in the nutrient content, changes which may have obscured the significant relationship between snail body size and snail P content I expected in this study.

4.5 Conclusion

This study described the elemental composition of aquatic snails and their potential food sources in spring ecosystems differing in physical and chemical water quality.The elemental composition of snails varied widely and was related to taxonomy but not necessarily their food sources. Differences in the P content of the same species collected from multiple springs were also attributed to water temperature, which *Pyrgulopsis* from cold springs had significantly higher body P content compared to conspecifics from warm springs. Further, elemental imbalances were significantly higher in warm springs compared to cold springs. However, to clarify whetherthese patterns arose exclusively from differences in water temperature needs to be further verified. The variability of elemental composition of aquatic snails studied in this dissertationlikely have consequences for a number of ecological processes, such as foraging strategies, biogeochemical cycling, competition, and their sensitivity towards disturbances. For example, if snails in springs are adapted over long time periods to lower nutrient supplies, anthropogenic impacts in the form of excessive nutrient inputs can dramatically affect the entire ecosystem as documented by experiments (see Elser et al. 2005) by retarding snail growth and increasing snail mortality.

CHAPTER 5

CONCLUSIONS AND RECOMMENDATIONS

The research presented in this dissertation consisted of three parts: 1) Trophic relationships between benthic macroinvertebrates and their food sources along a land use gradient in the Walker River; 2) the effect of habitat characteristics on biodiversity and secondary production assessment in the Walker River and 3) Great Basin springs ecosystems: A case study using ecological stoichiometry.

The first study (Chapter 2) focused on the elemental composition of BMI and their potential food resources along a land use gradient in Walker River to understand the trophic relationship using ecological stoichiometry. Temporal and spatial variation was observed in the elemental composition of basal food resource, while the elemental composition of BMI varied less along the land use gradient. While elemental composition of basal food resource was partly related to land use (forests, urban and agricultural areas), the elemental composition of BMI varied less among nutrient rich and nutrient-poor sites and indicated that taxonomy, allometry and feeding mode (FFG) are important factors.Elemental imbalances between FFG’s and their potential food resources were evident even at nutrient-enriched sites, however a clear spatial pattern along the land use gradient was not observed.High seasonal variability in nutrient inputs and consequently in the basal food resources might beone reason that obscured clear patterns.Considering spatial and temporal changes due to variation in nutrient inputs and alterations in the natural hydrograph seem to be important to understand trophic interactions in semi-arid watersheds with different land use types.

The second study (Chapter 3) investigated changes in biodiversity of BMI along the Walker River by applying different biotic indices. Further, indices and BMI biomass estimates were related to habitat characteristics. Secondary production was estimatedfor *Baetis* populations at two sites in Walker River differing in nutrient concentration to assess effects of nutrient pollution on BMI. The study showed that biodiversity decreased downstream with increase of pollutant tolerant taxa. This was related to stream width, substrate size, stream temperature and nutrients.BMI biomass varied spatially and temporally along Walker River. Interestingly, BMI density and biomass were not different between nutrient-rich site (EWB) and nutrient-poor site (WWB).However, the Shannon-Wiener-Index indicated thatsimilar density at site EWB was caused by a lower number of species.

Baetis secondary production at site EWB (1.3 g/m^2yr^{-1}) was higher compared to the site WWB (0.7g/m^2yr^{-1}) which might be related to higher food quality and warmer stream temperature. However, results should be used with caution because the sampling period was relatively short.High discharge due to water releases from reservoirs for irrigation purposes prevented sampling on same dates.Results from this study can be used as a basis for restoration and management practices. Results indicate that not only an increase of discharge should be considered to improve biodiversity, but also effect of substrate should also be considered. Other previous studies on stream restorationhave also emphasized effects of large woody debris and rocks by creating microhabitats.Also riparian vegetation will be a good addition for providing shading effects on thestream temperature.

The third study (Chapter 4) focused on the elemental composition of aquatic snails and their potential food source in a variety of spring ecosystems differing in physic-chemical habitat characteristics. Snails varied more in their bod N and P contents than their C content. The elemental composition appeared to be related to taxonomy; however a clear trend was not found between the four snail families investigated in this study. Interestingly, even the same species collected in multiple springs differed significantly in their elemental composition supporting an assumption of recent ecological stoichiometric models that, BMI can deviate from strict homeostasis depending on the environment they are living in. It appears that the water temperature had an effect on the elemental composition of *Pyrgulopsis* spp.

The body P content in individuals from warm springs (water temperature > 20ºC) was significantly lower compared to that from cold springs. Also elemental imbalances between snails and their food source were significantly higher in warm springs compared to those in cold springs. Whether differences in the snail body P content is caused by intrinsic factors due to the long-term acclimation to temperature or if it is caused by an adaption of feeding on different food quality should be addresses in future studies. Results from this study can be used to initiate future research on food web dynamics in springs to improve the mechanistic understanding of the elemental dynamics in these understudied aquatic ecosystems. Due to a more stable discharge and physico-chemical water quality other factors might be affecting the food web dynamic in springs compared to lotic and lentic ecosystems.

5.1 Recommendations for Future Research

5.1.1 Chapter 2

The results from this study are based on the assumption that BMI feed on exactly the same basal food and it is difficult to assess what is actually being eaten. Gut contentcoupled with nitrogen and carbon isotope analyses can be helpful to clarify the origin of basal food resources (allochthonous versus authochthonous matter). Therefore using elemental mismatches to assess if consumer growth is limited by their food source should be used with caution. To assess effects of elemental mismatches between producer and consumer on BMI growth and reproduction experiments with similar sized individuals feeding on the same food source can be helpful to solve these uncertainties.

5.1.2 Chapter 3

The results from the secondary production on *Baetis* population are based on short-term evaluation and likely underestimated annual production. Therefore, future research should consider long-term (at least 12 months) samples to assess secondary production to include all cohorts over the period of one year.Short term sampling (< 12 months)would also be sufficient if sampling occurs on shorter time intervals. Our results also indicate that secondary production of the same species can vary even within the same stream. Therefore, calculating an overall mean may sometimes led to biased information about ecosystem integrity. Therefore future studies should estimate secondary production for the most important constituent habitats.

5.1.3 Chapter 4

The results from this study are based on one sampling event during the summer months. Although springs are very stable ecosystems in terms of physicochemical environments; long-term monitoring of springs are recommended to account for changes in snail and their potential food source elemental composition due to variables not captured in this study, e.g. differences in day length over the period of one year might affect periphyton and algae growth and consequently its elemental composition.

Laboratory experiments or field experiments using enclosures are highly recommended for future research tobetter discern between water temperature and food quality effects on the body elemental stoichiometry of spring snails. Results from these experiments would help to understand anthropogenic impacts, such as changes in water temperature of springs due to water withdrawal (decreasing the volume) or climate change.

In a few springs investigated in this dissertation,some snail species, such as the exotic snail *Melanoides tuberculata* was the dominant invertebrate and reached very high densities and may constitute a major pool of nitrogen and phosphorus as observed for other invasive snail species in some streams(Hall et al., 2003). Future studies should particularly determine the role of exotic snails on N and P fluxes in spring ecosystems to assess the contribution of those snails and potential consequences of ecosystem function, food web dynamic and element availability. Also, additional genetic analyses among same population found in springs differing widely in environmental variables would help to determine how much phylogeny would help to explain patterns in the elemental composition of related species.

APPENDIX A. WALKER RIVER WATER QUALITY DATA, BASAL FOOD SOURCES AND BENTHIC MACROINVERTEBRATES

i) Nitrite-nitrogen and nitrate-nitrogen (NO_3-N+NO_2-N), ammonia-nitrogen (NH_3-N), dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), total phosphorus (TP), dissolved organic carbon (DOC), and total suspended solids (TSS) concentrations from the six sites sampled in spring and eighth sites sampled in summer and fall along the east Walker River (EWC, EWB, EWA), the west Walker River (WWC, WWB, WWA), and the main stem of the Walker River (WD, WC).

Sampling Site	**Sampling Season**	**NO_3-N+NO_2-N**	**NH_3-N**	**DIN**	**SRP**	**TP**	**DOC**	**TSS**
		μg/l					**mg/l**	
WC	Spring	22	8	30	35	89	3.4	27.8
WD	Spring	34	7	41	33	129	4.0	62.0
EWA	Spring	7	7	14	31	122	4.2	72.7
EWB	Spring	7	13	20	10	38	4.6	6.0
WWA	Spring	33	11	44	31	102	4.6	36.2
WWB	Spring	24	7	31	3	61	2.7	41.0
WC	Summer	10	12	22	52	74	3.1	12.0
WD	Summer	39	11	50	48	108	3.2	44.6
EWA	Summer	32	11	43	81	131	5.0	38.8
EWB	Summer	91	37	128	105	138	5.7	6.0
EWC	Summer	6	6	12	7	12	1.0	2.8
WWA	Summer	22	10	32	30	86	3.3	43.4
WWB	Summer	5	4	9	8	13	1.3	2.0
WWC	Summer	8	5	13	6	10	0.5	1.4
WC	Fall	71	10	81	38	77	3.3	22.4
WD	Fall	73	11	84	34	67	3.5	18.6
EWA	Fall	51	12	63	39	73	5.2	15.3
EWB	Fall	108	44	152	58	92	7.0	3.4
EWC	Fall	8	7	15	6	9	0.8	0.5
WWA	Fall	52	9	61	22	41	2.8	7.4
WWB	Fall	7	5	12	9	14	1.3	0.7
WWC	Fall	6	6	12	4	6	0.2	0.2

Note: Site codes, (WC = Walker C, WD = Walker D, EWA = East Walker River A, EWB = East Walker River B, EWC = East Walker River C, WWA = West Walker River A, WWB = West Walker River B, WWC = West Walker River C.

ii) Periphyton and seston %C, %N, %P, C:N, C:P, and N:P ratios from the six sites sampled in spring and eighth sites sampled in summer and fall along the east Walker River (EWC, EWB, EWA), the west Walker River (WWC, WWB, WWA), and the main stem of the Walker River (WD, WC).

Sampling Site	**Sampling Season**	**Food Source**	**C**	**N**	**P**	**C:N**	**C:P**	**N:P**
			(%)			**(molar)**		
WD	Spring	Periphyton	0.15	6	0.82	7	109	12
EWA	Spring	Periphyton	0.17	9	0.95	12	139	13
EWB	Spring	Periphyton	0.25	16	1.75	11	168	16
WWA	Spring	Periphyton	0.16	10	1.13	11	197	17
WWB	Spring	Periphyton	0.12	20	1.81	13	427	33
WC	Summer	Periphyton	0.15	13	1.09	14	228	16
WD	Summer	Periphyton	0.20	30	3.24	11	391	36
EWA	Summer	Periphyton	0.18	12	1.27	11	168	16
EWB	Summer	Periphyton	0.25	30	2.91	12	309	26
EWC	Summer	Periphyton	0.19	19	1.53	14	253	18
WWA	Summer	Periphyton	0.16	20	2.06	11	322	28
WWB	Summer	Periphyton	0.23	8	0.79	11	87	8
WWC	Summer	Periphyton	0.20	19	1.25	18	246	14
WD	Fall	Periphyton	0.16	7	0.65	12	107	9
EWA	Fall	Periphyton	0.15	10	1.10	10	169	16
EWB	Fall	Periphyton	0.21	28	2.90	11	338	31
EWC	Fall	Periphyton	0.15	13	1.46	11	228	22
WWA	Fall	Periphyton	0.21	14	1.27	13	173	13
WWB	Fall	Periphyton	0.18	11	1.37	9	155	17
WWC	Fall	Periphyton	0.19	20	1.69	14	277	20
WC	Spring	Seston	0.26	30	1.44	25	351	15
WD	Spring	Seston	0.15	28	1.49	29	478	21
EWA	Spring	Seston	0.12	23	1.03	28	495	18
EWB	Spring	Seston	0.18	27	2.98	11	391	37
WWA	Spring	Seston	0.18	21	1.78	14	320	23
WWB	Spring	Seston	0.15	33	1.66	23	561	25
WD	Summer	Seston	0.18	27	1.97	16	394	24
EWA	Summer	Seston	0.18	25	1.37	21	354	17
EWB	Summer	Seston	0.31	29	3.48	10	239	25
EWC	Summer	Seston	0.11	26	1.15	27	614	23
WWA	Summer	Seston	0.15	23	1.71	16	403	25
WWB	Summer	Seston	0.12	28	1.63	20	591	30
WWC	Summer	Seston	0.15	12	0.53	26	204	8
WC	Fall	Seston	0.17	22	0.96	27	339	12
WD	Fall	Seston	0.14	24	1.68	17	439	27
EWA	Fall	Seston	0.13	24	1.34	21	468	23
EWB	Fall	Seston	0.17	31	4.00	9	473	52
EWC	Fall	Seston	0.08	28	1.31	25	900	36
WWA	Fall	Seston	0.13	15	0.90	20	302	15
WWB	Fall	Seston	0.17	25	1.75	17	382	23
WWC	Fall	Seston	0.17	7	0.77	10	104	10

iii) Benthic macroinvertebrate species and assigned functional feeding groups (FFG) from the six sites sampled in spring and eighth sites sampled in summer and fall along the east Walker River (EWC, EWB, EWA), the west Walker River (WWC, WWB, WWA), and the main stem of the Walker River (WD, WC).

Sampling Site	Season	Species	FFG
EWA	Fall	*Hydropsyche*	CF
EWA	Fall	*Cheumatopsyche*	CF
EWA	Fall	*Doroneuria*	PR
EWA	Fall	*Heptagenia*	SC
EWB	Fall	*Hydropsyche*	CF
EWB	Fall	*Simulium*	CF
EWB	Fall	*Amiocentrus*	CG
EWB	Fall	*Baetis tricaudatus*	CG
EWB	Fall	*Baetis tricaudatus*	CG
EWB	Fall	*Ameletus*	CG
EWB	Fall	*Skwala*	PR
EWB	Fall	*Calineuria*	PR
EWB	Fall	*Menetus*	SC
EWB	Fall	*Physa*	SC
EWB	Fall	*Hyalella*	SH
EWC	Fall	*Anctopsyche*	CF
EWC	Fall	*Serratella*	CG
EWC	Fall	*Siphlonurus*	CG
EWC	Fall	*Rhyacophila*	PR
EWC	Fall	*Sweltsa*	PR
EWC	Fall	*Orohermes*	PR
EWC	Fall	*Cinygmula*	SC
WC	Fall	*Corbicula*	CF
WC	Fall	*Centroptilum*	CG
WC	Fall	*Argia*	PR
WD	Fall	*Corbicula*	CF
WD	Fall	*Baetis tricaudatus*	CG
WD	Fall	*Tricorythodes*	CG
WWA	Fall	*Hydropsyche*	CF
WWA	Fall	*Corbicula*	CF
WWA	Fall	*Anodonta californica*	CF
WWA	Fall	*Tricorythodes*	CG
WWA	Fall	*Baetis tricaudatus*	CG

Sampling Site	**Season**	**Species**	**FFG**
WWA	Fall	*Ophiogomphus*	PR
WWA	Fall	*Hesperoperla*	PR
WWB	Fall	*Hydropsyche*	CF
WWB	Fall	*Ameletus*	CG
WWB	Fall	*Serratella*	CG
WWB	Fall	*Timpanoga*	CG
WWB	Fall	*Hexatoma*	PR
WWB	Fall	*Dicranota*	PR
WWB	Fall	*Dicosmoecus*	SH
WWC	Fall	*Brachycentrus*	CF
WWC	Fall	*Baetis tricaudatus*	CG
WWC	Fall	*Serratella*	CG
WWC	Fall	*Attenella*	CG
WWC	Fall	*Siphlonurus*	CG
WWC	Fall	*Timpanoga*	CG
WWC	Fall	*Calineuria*	PR
WWC	Fall	*Hexatoma*	PR
WWC	Fall	*Rhyacophila*	PR
WWC	Fall	*Cinygmula*	SC
EWA	Spring	*Ephemerella*	CG
EWA	Spring	*Baetis*	CG
EWB	Spring	*Corbicula*	CF
EWB	Spring	*Hydropsyche*	CF
EWB	Spring	*Ephemerella*	CG
EWB	Spring	*Ephemerella*	CG
EWB	Spring	*Hyalella*	SH
WC	Spring	*Tricorythodes*	CG
WC	Spring	*Ephemerella*	CG
WC	Spring	*Ameletus*	CG
WC	Spring	*Isoperla*	PR
WD	Spring	*Hydropsyche*	CF
WD	Spring	*Empehmerella*	CG
WD	Spring	*Isoperla*	PR
WD	Spring	*Ophiogomphus*	PR
WWB	Spring	*Ephemerella*	CG
WWB	Spring	*Drunella grandis*	CG
WWB	Spring	*Ameletus*	CG
WWB	Spring	*Calineuria*	PR
EWA	Summer	*Corbicula*	CF

Sampling Site	**Season**	**Species**	**FFG**
EWA	Summer	*Hydropsyche*	CF
EWA	Summer	*Heptagenia*	SC
EWB	Summer	*Fallceon quirlleri*	CG
EWB	Summer	*Hyalella*	CG
EWB	Summer	*Epeorus*	SC
EWC	Summer	*Attenella*	CG
EWC	Summer	*Ameletus*	CG
EWC	Summer	*Calineuria*	PR
EWC	Summer	*Sweltsa*	PR
EWC	Summer	*Orohermes*	PR
EWC	Summer	*Epeorus*	SC
EWC	Summer	*Yoraperla*	SH
WC	Summer	*Baetis tricaudatus*	CG
WC	Summer	*Tricorythodes*	CG
WC	Summer	*Brachycercus*	CG
WC	Summer	*Fossaria*	SC
WC	Summer	*Physa*	SC
WD	Summer	*Baetis ssp.*	CG
WWA	Summer	*Hydropsyche*	CF
WWA	Summer	*Baetis tricaudatus*	CG
WWA	Summer	*Hydropsyche*	CG
WWA	Summer	*Baetis tricaudatus*	CG
WWA	Summer	*Ophiogomphus*	PR
WWA	Summer	*Ophiogomphus*	PR
WWB	Summer	*Stictotarsus*	CF
WWB	Summer	*Brachycentrus*	CF
WWB	Summer	*Hydropsyche*	CF
WWB	Summer	*Drunella grandis*	CG
WWB	Summer	*Drunella colorado*	CG
WWB	Summer	*Dicranota*	PR
WWB	Summer	*Epeorus*	SC
WWB	Summer	*Dicosmoecus*	SH
WWC	Summer	*Brachycentrus*	CF
WWC	Summer	*Ameletus*	CG
WWC	Summer	*Drunella*	CG
WWC	Summer	*Attenella*	CG
WWC	Summer	*Serratella*	CG
WWC	Summer	*Dicranota*	PR

Sampling Site	**Season**	**Species**	**FFG**
WWC	Summer	*Hexatoma*	PR
WWC	Summer	*Calineuria*	PR
WWC	Summer	*Rithrogena*	SC

APPENDIX B. WALKER RIVER BIODIVERSITY AND SECONDARY PRODUCTION

i) Benthic macroinvertebrates and their assigned tolerances values from the six sites sampled in spring and eighth sites sampled in summer and fall along the east Walker River (EWC, EWB, EWA), the west Walker River (WWC, WWB, WWA), and the main stem of the Walker River (WD, WC).

Sampling Site	**Season**	**Species**	**Tolerance Values**
WC	Spring	*Baetis tricaudatus*	5
WC	Spring	*Callibaetis*	5
WC	Spring	*Caenis*	6
WC	Spring	*Isoperla*	2
WD	Spring	*Baetis spp.*	5
WD	Spring	*Ephemerella dorothea*	1
WD	Spring	*Heptageniidae*	3
WD	Spring	*Tricorythodes*	4
WD	Spring	*Hydroptila*	4
WD	Spring	*Leptoceridae*	4
WWA	Spring	*Baetidae*	5
WWA	Spring	*Ephemerella excrucians*	1
WWA	Spring	*Heptageniidae*	3
WWA	Spring	*Tricorythodes*	4
WWA	Spring	*Isoperla*	2
WWA	Spring	*Culoptila*	1
WWA	Spring	*Hydropsyche*	4
WWA	Spring	*Oecetis*	4
EWB	Spring	*Baetis tricaudatus*	5
EWB	Spring	*Drunella flavilinea*	1
EWB	Spring	*Ephemerella inermis*	1
EWB	Spring	*Tricorythodes*	4
EWB	Spring	*Isoperla*	2
EWB	Spring	*Brachycentrus*	1
EWB	Spring	*Glossosoma*	1
EWB	Spring	*Hydroptila*	4
EWB	Spring	*Ceraclea*	4
EWB	Spring	*Optioservus*	4

Sampling Site	**Season**	**Species**	**Tolerance Value**
WWB	Spring	*Baetis tricaudatus*	5
WWB	Spring	*Attenella delantala*	1
WWB	Spring	*Caudatella heterocaudata*	1
WWB	Spring	*Drunella flavinea*	1
WWB	Spring	*Drunella grandis*	1
WWB	Spring	*Ephemerella excrucians*	1
WWB	Spring	*Epeorus*	3
WWB	Spring	*Rithrogena*	3
WWB	Spring	*Perlodidae*	2
WWB	Spring	*Cultus sp.*	2
WWB	Spring	*Skwala sp.*	2
WWB	Spring	*Glossosoma*	1
WWB	Spring	*Glossosoma sp.*	1
WWB	Spring	*Ceratopsyche*	4
WWB	Spring	*Lepidostoma sp.*	1
WWB	Spring	*Neophylax*	3
WWB	Spring	*Oreodytes, adult*	5
WWB	Spring	*Optioservus quadrimeculatus*	4
WC	Summer	*Centroptilum/Procloeon*	5
WC	Summer	*Fallceon quilleri*	5
WC	Summer	*Tricorythodes*	4
WD	Summer	*Fallceon quilleri*	5
WD	Summer	*Heptageniidae*	3
WD	Summer	*Tricorythodes*	4
WD	Summer	*Hydroptila*	4
WWA	Summer	*Acentrella*	5
WWA	Summer	*Baetis tricaudatus*	5
WWA	Summer	*Camelobaetidius warreni*	5
WWA	Summer	*Centroptilum/Procloeon*	5
WWA	Summer	*Paracloeodes*	5
WWA	Summer	*Tricorythodes*	4
WWA	Summer	*Agapetus*	1
WWA	Summer	*Cheumatopsyche*	4
WWA	Summer	*Hydropsyche*	4
WWA	Summer	*Hydroptila*	4
WWA	Summer	*Nectopsyche*	4
EWB	Summer	*Baetis tricaudatus*	5
EWB	Summer	*Fallceon quilleri*	5
EWB	Summer	*Tricorythodes*	4

Sampling Site	**Season**	**Species**	**Tolerance Value**
EWB	Summer	*Amiocentrus*	1
EWB	Summer	*Hydropsyche*	4
EWB	Summer	*Hydroptila*	4
EWB	Summer	*Leptoceridae (Distinct)*	4
EWB	Summer	*Optioservus*	4
EWB	Summer	*Zaitzevia*	4
WWB	Summer	*Ameletus*	1
WWB	Summer	*Acentrella*	5
WWB	Summer	*Baetis bicaudatus*	5
WWB	Summer	*Fallceon quilleri*	5
WWB	Summer	*Attenella delantala*	1
WWB	Summer	*Drunella spp.*	1
WWB	Summer	*Ephemerella aurivillii*	1
WWB	Summer	*Ephemerella infrequens*	1
WWB	Summer	*Serratella tibialis*	1
WWB	Summer	*Timpanoga*	1
WWB	Summer	*Cinygmula*	3
WWB	Summer	*Epeorus*	3
WWB	Summer	*Paraleptophlebia*	3
WWB	Summer	*Sweltsa*	0
WWB	Summer	*Isoperla*	2
WWB	Summer	*Dicosmoecus*	3
WWB	Summer	*Nebrioporus/ Stictotarsus*	5
WWB	Summer	*Optioservus quadrimeculatus*	4
WC	Fall	*Acerpenna*	5
WD	Fall	*Fallceon quilleri*	5
WD	Fall	*Tricorythodes*	4
WWA	Fall	*Acerpenna*	5
WWA	Fall	*Acentrella*	5
WWA	Fall	*Baetis tricaudatus*	5
WWA	Fall	*Camelobaetidius warreni*	5
WWA	Fall	*Fallceon quilleri*	5
WWA	Fall	*Tricorythodes*	4
WWA	Fall	*Perlodidae*	2
WWA	Fall	*Protoptila*	1
WWA	Fall	*Hydropsyche*	4
WWA	Fall	*Hydroptila*	4
WWA	Fall	*Oecetis*	4
EWB	Fall	*Baetis tricaudatus*	5

Sampling Site	**Season**	**Species**	**Tolerance Value**
EWB	Fall	*Camelobaetidius warreni*	5
EWB	Fall	*Fallceon quilleri*	5
EWB	Fall	*Labiobaetis*	5
EWB	Fall	*Ephemerellidae (Distinct)*	1
EWB	Fall	*Cinygmula*	3
EWB	Fall	*Tricorythodes*	4
EWB	Fall	*Amiocentrus*	1
EWB	Fall	*Brachycentrus*	1
EWB	Fall	*Hydropsyche*	4
EWB	Fall	*Hydroptila*	4
EWB	Fall	*Lepidostoma*	1
EWB	Fall	*Oecetis*	4
EWB	Fall	*Optioservus quadrimeculatus*	4
EWB	Fall	*Zaitzevia*	4
WWB	Fall	*Ameletus*	1
WWB	Fall	*Acentrella*	5
WWB	Fall	*Baetis bicaudatus*	4
WWB	Fall	*Baetis tricaudatus*	4
WWB	Fall	*Fallceon quilleri*	5
WWB	Fall	*Attenella delantala*	1
WWB	Fall	*Serratella michneri*	1
WWB	Fall	*Timpanoga hecuba hecuba*	1
WWB	Fall	*Rithrogena*	3
WWB	Fall	*Tricorythodes*	4
WWB	Fall	*Paraleptophlebia*	3
WWB	Fall	*Capniidae*	2
WWB	Fall	*Sweltsa*	0
WWB	Fall	*Perlinodes aurea*	2
WWB	Fall	*Skwala*	2
WWB	Fall	*Amiocentrus*	1
WWB	Fall	*Glossosoma*	1
WWB	Fall	*Hydropsychidae*	4
WWB	Fall	*Hydroptila*	4
WWB	Fall	*Lepidostoma*	1
WWB	Fall	*Limnephilidae*	3
WWB	Fall	*Neophylax*	3
WWB	Fall	*Oreodytes*	5
WWB	Fall	*Optioservus*	4
WWB	Fall	*Zaitzevia*	4

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PUBLICATIONS

Mehler, K., Acharya, K., Sada, D. and Z. Yu. 2012. Spatial and temporal variation in elemental composition of basal resources and benthic macorinvertebrates along a land use gradient in a Great Basin watershed. Hydrobiologia (under review).

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