

AN ABSTRACT OF THE THESIS OF

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presented on February 8, 2011.

Title: A Food Web Analysis of a Mojave Desert Geothermal Spring System and Feeding Ecology of Moapa Dace (*Moapa coriacea*)

Abstract approved:

Stanley V. Gregory

Understanding food webs is fundamental in conserving endangered species and maintaining healthy ecosystem function, particularly in desert spring systems. We identified dominant energy sources in the Muddy River Warm Springs area, Clark County, NV using carbon and nitrogen natural abundance stable isotope analyses. We examined isotopic signatures of specific macroinvertebrate food resources for the endangered, drift-feeding Moapa dace (*Moapa coriacea*) and looked for changes in isotopic ratios over the stream gradient. Our results indicate the Muddy River Warm Springs area is supported primarily by allochthonous energy sources, and Moapa dace did not focus on specific macroinvertebrate taxa. We characterized a pattern of downstream $\delta^{13}\text{C}$ enrichment, which is seemingly common in groundwater-fed systems but discussed very little in the literature. We conclude that ground water carbon of marine origin, heterotrophic respiration, and fractionation and depletion of the $\delta^{13}\text{C}$ pool by autotrophs contribute to a wide range $\delta^{13}\text{C}$ values in primary producers and to the downstream enrichment pattern in the Muddy River Warm

Springs. We then quantified macroinvertebrate drift throughout the Moapa dace's current and historic range within the Muddy River Warm Springs. We examined the relationship of total drift biomass and temperature and associations between specific macroinvertebrate orders and Moapa dace abundance. We also explored habitat characteristics associated with Moapa dace and their prey. In 2008 and 2009, total drift biomass/time and the biomass of most orders was negatively correlated with temperature and positively correlated with discharge. Only Lepidoptera and Neotaenioglossa had positive associations with temperature in 2008. In 2009, total biomass/volume had a negative linear relationship with temperature and a positive linear relationship with discharge, though these relationships were absent in 2008. Moapa dace were associated with high temperatures, low stream discharge, shallow depth, and low drift biomass both years. They were positively associated with thermally tolerant Lepidoptera and Neotaenioglossa in 2008 and no orders in 2009. Macroinvertebrate drift may be greater in cooler, downstream reaches because temperatures in those reaches are favorable to more taxa, there is more cumulative benthic area contributing to production, and there are fewer drift feeding insectivores. Lastly, we examined Moapa dace feeding flexibility by experimentally manipulating drift (0, 34, 64, 100, and 200% of the natural drift level) and quantified their feeding attempts and success. We found that Moapa dace are obligate drift feeders, selecting drift 40 times more frequently than benthos. They did not adaptively shift foraging modes from drift to benthic when drift was experimentally reduced. Drift feeding rate increased in response to increasing drift, but drift feeding success only increased from

the 0% to the 64% drift level and did not change in the 100% and 200% levels. No relationship between fish size or food availability and aggression was detected.

Moapa dace may share an interspecific foraging association with sympatric White River springfish (*Crenichthys baileyi*). Moapa dace are currently excluded from lower, more productive reaches by invasive species and fish barriers. Maintaining spring flows, eradicating non-natives, and restoring system connectivity will likely benefit Moapa dace and other Muddy River Warm Springs endemics.

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A Food Web Analysis of a Mojave Desert Geothermal Spring System and
Feeding Ecology of Moapa Dace (*Moapa coriacea*)

by
Adam StSaviour

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented February 8, 2011
Commencement June 2011

Master of Science thesis of Adam StSaviour presented on February 8, 2011.

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Adam StSaviour, Author

ACKNOWLEDGEMENTS

Many thanks to my committee, Dr. Joe Ebersole (EPA), Dr. Dave Lytle, (Zoology), and Dr. Stan Gregory (Fisheries and Wildlife, major professor) for guidance and support. Stan generously gave his time helping me develop and complete this thesis. A very special thanks to Dr. Matt Mesa (USGS, Western Fisheries Research Center, Columbia River Research Lab) for taking a chance on me and supporting this work through a research assistantship. Thanks to Chris Dixon (USGS), Allison Manwaring (Great Basin Institute), and Cailin Doyle (SNWA) for field assistance and good company. Thanks to Bill Gerth (OSU) for aid in identifying macroinvertebrates. Thanks to Becky Flitcroft and Bruce McCune for statistical advice. Thanks to Erin Boyle (USFWS) for GIS assistance. Thanks to all of my wonderful Corvallis friends who kept me occupied when not working on my thesis.

Thank you to those who inspired me to believe that I can achieve anything if I work hard enough at it, especially my father, Albert StSaviour, and my first supervisor Paul Johnson (Maine Inland Fisheries and Wildlife, retired). This experience has enabled me to grow tremendously, both personally and professionally.

CONTRIBUTION OF AUTHORS

S.V. Gregory contributed to the study design in Chapters 2, 3, and 4. S.V. Gregory contributed to data analyses and interpretation in Chapters 2, 3, and 4, and R.L.

Flitcroft contributed to statistical analyses in Chapter 4. S.V. Gregory contributed to the editing of draft manuscripts for chapters.

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CHAPTER 1: INTRODUCTION

Ecological interactions in the aquatic environment are both fascinating and essential to maintaining landscape ecosystem function (Nakano and Murakami 2001). As human population has grown, demand for freshwater has stressed some aquatic systems beyond sustainable limits, which is especially evident in arid regions (Deacon et al. 2007, Olden et al. 2008). Desert spring systems are some of the world's most endangered habitats. They are associated with a high degree of endemism and endangered species. Desert fishes account for two-thirds of all endangered fish species in North America (Williams et al. 1989, Helfman et al. 2009a). They are susceptible to extinction because they frequently have small populations, restricted distributions, and specialized feeding strategies. In addition, habitat degradation, competition with invasive species, and reduced stream flows as a result of regional water withdrawals for human use extensively impact fish populations in arid regions (Deacon et al. 2007, Olden et al. 2008).

In 2008, the U.S. Geological Survey started a research program designed to determine the potential effects of reduced spring flows, as a result of regional ground water withdrawal, on the aquatic community of the Muddy River Warm Springs area, Clark County, NV. Of particular interest was how an altered hydrologic regime would change the thermal profile of this system and how endemic thermophilic inhabitants would respond. These inhabitants include the endangered Moapa dace (*Moapa coriacea*) and several species of concern, a springfish and five macroinvertebrates. In conjunction with a hydraulic modeling effort and population viability analysis, I

examined the Muddy River Warm Springs food web and feeding ecology of Moapa dace. The purpose was to understand how Moapa dace might respond to changes in food resources as a result of changes in spring flows. Knowledge of food web structure is fundamental for conserving endangered species and maintaining ecosystem function (Allan and Flecker 1993, Chapin III et al. 2000). Our findings will help resource managers make informed decisions about water use, endangered species recovery, and habitat restoration.

This research was structured hierarchically. In chapter 2, we examined the basic framework of the Muddy River Warm Springs food web using stable isotope analyses. We identified the primary nutrient sources for this system and documented changes in isotopic signatures along the stream course. We also examined specific food resources used by the insectivorous, drift-feeding Moapa dace. In chapter 3, we investigated whether the macroinvertebrate orders identified as significant Moapa dace food resources in chapter 2 corresponded with the most abundant macroinvertebrate orders available in the drift. This was accomplished by quantifying macroinvertebrate drift throughout the spring system to locate where drift was most abundant and which macroinvertebrate orders were most abundant in drift and, thus, most available to Moapa dace. In addition, we quantified the relationship between drift and temperature and explored associations between 17 other habitat variables and abundances of Moapa dace and their important food resources. In chapter 4, we tested whether Moapa dace would respond to a reduction in drift by shifting their feeding behavior. We observed Moapa dace feeding behavior at five experimentally manipulated levels

of drift, measuring both drift and benthic feeding frequency and success. Finally, we explored whether the Moapa dace displayed a relationship between level of aggression and their size or the drift level.

CHAPTER 2: A STABLE ISOTOPE FOOD WEB ANALYSIS OF A MOJAVE
DESERT GEOTHERMAL SPRING SYSTEM

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Abstract. Understanding food webs is fundamental in conserving endangered species and maintaining healthy ecosystem function, particularly in desert spring systems. We identified dominant energy sources in the Muddy River Warm Springs area, Clark County, NV using carbon and nitrogen natural abundance stable isotope analyses. We examined isotopic signatures of specific macroinvertebrate food resources for the endangered Moapa dace (*Moapa coriacea*) and looked for changes in isotopic ratios over the stream gradient. Our results indicate the Muddy River Warm Springs area is supported primarily by allochthonous energy sources, despite its small size and relatively open canopy. In addition, *M. coriacea* did not focus on specific macroinvertebrate taxa, suggesting they are general drift feeders. We characterized a pattern of downstream $\delta^{13}\text{C}$ enrichment, which is seemingly common in groundwater-fed systems but discussed very little in the literature. We conclude that ground water carbon of marine origin, equilibration of dissolved CO_2 , heterotrophic respiration, and fractionation and depletion of the $\delta^{13}\text{C}$ pool by autotrophs contribute to a wide range of $\delta^{13}\text{C}$ values in primary producers and to the downstream enrichment pattern in the Muddy River Warm Springs.

Key words: Moapa dace, *Moapa coriacea*, thermophilic, endemic, stable isotope, food web, autochthonous, allochthonous, trophic interaction

Desert spring systems are some of the world's most endangered habitats. They are associated with a high degree of endemism and endangered species. Desert fishes account for two thirds of all endangered fish species in North America (Williams et al. 1989, Helfman et al. 2009) They are susceptible to extinction because they frequently have small populations, restricted distributions, and specialized feeding strategies. In addition, habitat degradation, competition with invasive species, and reduced stream flows as a result of regional water withdrawals for human use impact fish populations in arid regions (Deacon et al. 2007, Olden et al. 2008). Knowledge of food webs is fundamental in conserving endangered species and maintaining ecosystem function (Allan and Flecker 1993, Chapin III et al. 2000) Groundwater, surface water, and riparian linkages are complex and unique from site to site in desert spring systems (Holmes et al. 1994, Bassett 2003, Doucett et al. 2007) As a result, food web knowledge of these types of systems is limited (Kennedy et al. 2005, Wilson and Blinn 2007).

Land use practices such as groundwater extraction and agricultural conversion may change food web dynamics in desert springs by altering spring discharges or riparian zones (Deacon and Bradley 1972, Sada and Herbst 1999, Patten et al. 2007). Riparian vegetation affects allochthonous and autochthonous food resources in spring systems by controlling delivery of light and terrestrial organic material to the stream (Gregory et al. 1991, Pusey and Arthington 2003).

Stable isotopes have proven valuable in understanding nutrient flow and trophic interactions in food webs. See Peterson and Fry (1987), Rounick and

Winterbourn (1986), and Fry (1991) for review of stable isotope techniques. Studies using stable isotope analyses elucidate linkages between riparian vegetation, in-stream producers, soil, groundwater, surface water, invertebrates, and fishes (Rounick and Winterbourn 1986, Junger and Planas 1994, Mulholland et al. 2000, Hall et al. 2001, McCutchan Jr. and Lewis Jr. 2002). Water chemistry, plant, and animal communities can change drastically over short distances in spring-fed desert streams. Stable isotopes are also useful for identifying changes in nutrient cycling and trophic dynamics on the fine spatial scales found in these types of systems (Kennedy et al. 2005, Doctor et al. 2008).

Stable isotopes can be used to determine the relative importance of autochthonous in-stream primary production versus allochthonous terrestrial inputs to aquatic food webs (Rounick and Winterbourn 1986, Finlay 2001, Minshall and Ruginski 2006). Autochthonous sources exhibit wide ranges of $\delta^{13}\text{C}$, from -46‰ to 0‰, but are often distinct and higher, or more enriched, than allochthonous sources. Allochthonous C₃ plant sources tend to have $\delta^{13}\text{C}$ ranges from -34 to -18‰ (Rounick and James 1984, Rounick and Winterbourn 1986, Fry 1991).

Observed differences in isotopic values of organisms can be attributed to a biological and physical process called fractionation. Plants incorporate more light carbon isotopes than heavy during photosynthesis because the light isotopes move across membranes more readily. Terrestrial C₃ plants fractionate carbon at a rate of about -20‰ from their source, atmospheric CO₂ with a value of -7‰ (Farquhar et al. 1982, Peterson and Fry 1987). Aquatic primary producers are more variable in how

much they fractionate. Once carbon has been incorporated into the food web, it fractionates very little as it cycles through to higher trophic levels at a rate of about +1‰ per trophic level (Rounick and Winterbourn 1986). An organism that has a more negative isotopic value compared to its source is said to be “depleted” where as one with a more positive value is said to be “enriched.” In contrast with carbon, nitrogen enriches at a rate of 3 to 4‰ with each increase in trophic level (Rounick and Winterbourn 1986, Post 2002, Peterson and Fry 1987).

Because carbon is relatively stable through the food web, it is used to indicate nutrient sources in isotope food web diagrams. When source values of $\delta^{13}\text{C}$ are distinct, one can easily determine which source a consumer is depending on by how closely matched their $\delta^{13}\text{C}$ values are to the particular sources (Rounick and Winterbourn 1986, Fry 1991). However, $\delta^{13}\text{C}$ values of primary producers can be quite variable. The total amount of dissolved inorganic carbon (DIC) available to an aquatic primary producer and the source $\delta^{13}\text{C}$ value of that DIC are the overriding factors that control $\delta^{13}\text{C}$ values of aquatic primary producers (Hecky and Hesslein 1995, Trudeau and Rasmussen 2003).

We used natural abundance carbon and nitrogen stable isotopes to develop a frame work of a poorly-understood desert warm spring food web. The food web analysis was conducted on the Warm Springs headwater region of the Muddy River near the town of Moapa, Clark County, Nevada. The Warm Springs area is home to an endemic and critically endangered cyprinid minnow, the Moapa dace (*Moapa coriacea*) (Scoppettone et al. 1998). There are also five thermophilic endemic

macroinvertebrates: two snails *Tryonia clathrata* and *Pyrgulopsis avernalis* a water bug *Limnocoris moapensis* and two elmid beetles *Microcylloepus moapensis* and *Stenelmis caiida moapa* (Scoppettone et al. 1994). *M. coriacea* were first collected in 1938 and described by Hubbs and Miller (1948). *M. coriacea* have had federal protected status since 1967 (U.S. Fish and Wildlife Service 2002). They co-exist in the Muddy River Warm Springs with the much more abundant native White River springfish (*Crenichthys baileyi*). The exotic, generalist, the short-finned molly (*Peocilia mexicana*) and small, exotic, predator, the mosquito fish (*Gambusia affinis*) are also present. Blue tilapia (*Oreochromis aureus*) are present below several fish passage barriers where they have displaced *M. coriacea* (Scoppettone et al. 2005). *M. coriacea* are thought to spawn year-round with only a few eggs developing at a time. Previous gut-contents analyses indicate an average composition of 75% macroinvertebrates and 25% plant material (Scoppettone et al. 1992). They are a highly active drift-feeding fish inhabiting an extreme thermal environment (Scoppettone 1993).

Considering the current status of *M. coriacea* and the paucity of information on the Muddy River Warm Springs food web, there is a need to better understand the food web in this desert spring ecosystem. We examined this food web using natural abundance carbon and nitrogen stable isotopes were used to test the following hypotheses: 1) *M. coriacea* depend on a food web supported by autochthonous production due to the relatively high nutritional value of algae. 2) *M. coriacea* exhibit stable isotope signatures that reflect secondary consumption of the most abundant

drifting invertebrate orders within their range. 3) Isotopic signatures of primary producers change along the stream course. We predicted upstream sites would exhibit a more depleted $\delta^{13}\text{C}$ signal than downstream sites due to the influence of geologic carbonate, and that there would be no change in $\delta^{15}\text{N}$ from upstream to down stream because nitrogen sources are unchanged.

Methods

Study Site

The Muddy River Warm Springs area is located in the Mojave Desert at 545 m elevation and 36°42'40.93"N 114°42'52.00"W latitude longitude. Average maximum and minimum air temperatures are 43.1 °C and 23.3 °C, respectively, in July and 16 °C and 0 °C in December. The Moapa area receives an average of 11 cm of precipitation annually, most of which falls in summer monsoon events (Community Environmental Monitoring Program 1999).

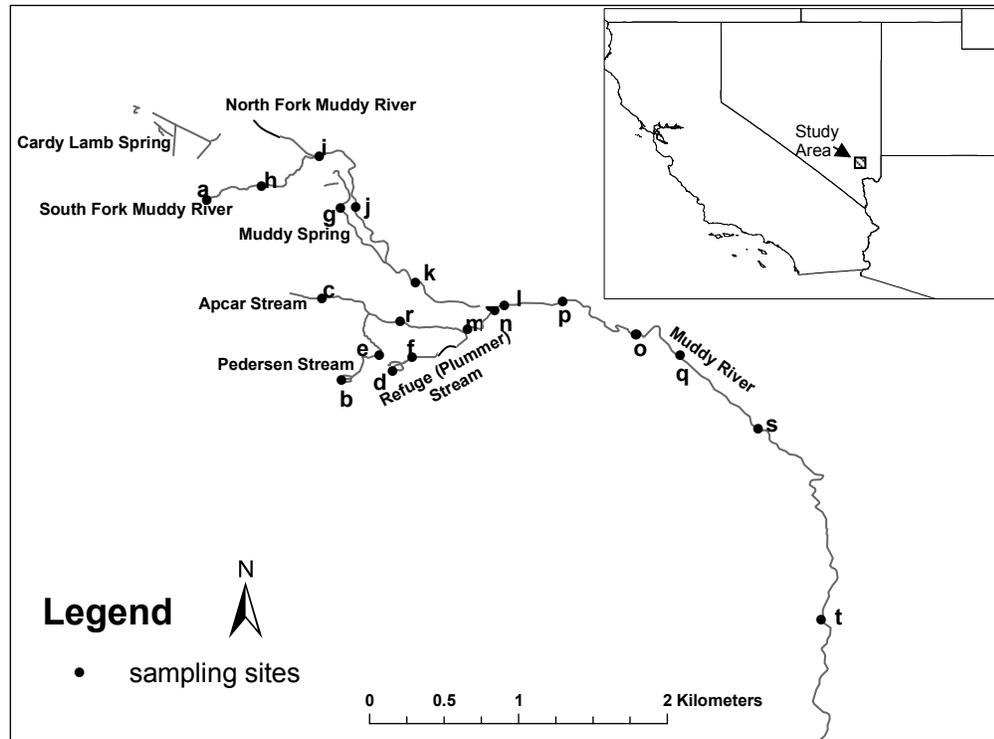


Fig.1: Upper Muddy River, Warm Springs Area, Clark County, NV, USA. Sampling sites are marked by solid circles and describe individually in Table 1.

Table 1: Sample site habitat characteristics. Substrate type codes: (0) Silt/clay (< 0.059 mm), (1) Sand (0.6-1 mm), (2) Gravel (2-15 mm), (3) Pebble (16-63 mm), (4) Cobble (64-256 mm), (5) Boulder (>256 mm), (6) Bedrock. Riparian species: P= Palm (*Washingtonia filifera*), T= Tamarisk (*Tamarix* spp.), A =Ash (*Fraxinus velutina*), M= Mesquite (*Prosopis* spp.), AW= Arrowweed (*Pluchea sericea*), C= Cattail (*Typha latifolia*), W = Willow (*Salix* spp.), G= Grass (*Sporobolus airoides*), WP= Water Pimpernell (*Samolis* spp.), O= Other

Site Code	Avg temp (°C)	Q(m ³ /s)	Habitat Unit type	Avg. Width (m)	Max depth (cm)	Mean depth (cm)	Dominant Substrate	% Embedd- edness	% Over- head cover	Riparian Species 1
a	31.73	0.0945	Run	2.4	67	40	0	10	60	P, T, M, C
b	31.33	0.0059	Riffle	0.9	13	12	3	20	0	AW, O
c	31.27	0.0405	Run	0.9	20	18	1	50	75	P
d	30.88	0.0604	Riffle	1	25	18	3	20	40	M, W, C, AW
e	30.99	0.0991	Run	1.6	28	22	3	20	30	A, C, WP
f	30.76	0.0925	Run	3.5	50	35	0	10	20	P, C
g	30.92	0.1579	Run	3.3	52	30	2	10	60	P, T
h	30.23	0.0936	Riffle	1.6	38	34	3	25	15	C, AW
i	29.70	0.2936	Riffle	4.5	38	16	2	30	60	P
j	29.29	0.4223	Riffle	5	40	30	2	20	60	P, T
k	29.19	0.6406	Glide	11.4	43	25	4	30	0	P, T, C, M
l	28.61	1.0045	Run	7.9	55	30	1	25	10	AW, W, T, O
m	28.44	0.2596	Run	2.3	60	60	1	20	90	A
n	27.71	0.2877	Glide	4.75	30	20	1	10	70	T, G, O
o	27.64	0.8711	Run	8	60	40	1	5	15	M, AW, T
p	28.20	0.7446	Riffle	8	65	40	1	25	10	T, AW, O
q	27.62	0.9062	Run	6	60	50	3	30	50	A, P, AW
r	27.72	0.1130	Riffle	1.25	12	12	3	40	75	A, O
s	27.17	0.9337	Riffle	4.9	46	29	3	90	20	P, AW, M, A
t	28.77	0.7163	Run	4	120	90	4	30	10	T, W, O

The Muddy River Warm Springs emanate from a deep Paleozoic carbonate aquifer. There are six spring areas within a 2-km radius with a cumulative discharge of 1.1 m³/s and little flow variation (Scoppettone, Burge, and Tuttle 1992). Temperatures of spring sources range from 31.0 to 32.0 °C with little annual variation (< 2.2 °C), and dissolved oxygen ranges from 4.1 to 6.2 mg/L (Scoppettone 1993). The calculated time that this water has traveled through the deep aquifer is between 9,000 and 12,000 years. The long exposure time to marine limestone is reflected in the DIC $\delta^{13}\text{C}$ value of Muddy River Warm Spring water, which is -6‰ (Bassett 2003).

Initial conservation efforts were targeted at land and water acquisition. The 47 ha Moapa Valley National Wildlife Refuge (MVNWR) was established in 1979 (U.S. Fish and Wildlife Service 2010). In 2007, the Southern Nevada Water Authority (SNWA) purchased the 477 ha Warm Springs Natural Area directly downstream of the MVNWR (Southern Nevada Water Authority 2009). There has been extensive habitat restoration occurring on both properties. Generally, the headwater springs on the MVNWR have a relatively open canopy and are dominated by native riparian shrubs and sedges. Within approximately 200 m the streams transition to greater canopy cover and are dominated by non-native fan palm (*Washingtonia filifera*). Conservation organizations have been restoring native vegetation while discouraging invasive plants.

Groundwater extraction for urban development threatens to reduce spring discharge, by reducing hydraulic head from the deep carbonate aquifer, a common problem in populated arid regions (Patten et al. 2007). A reduction in spring discharge

will likely lead directly to a reduction in overall aquatic habitat and in thermally suitable habitat for Moapa thermophilic endemics (Scoppettone et al. 2006).

Sample collection and processing

Samples for stable isotope analyses were collected from 20 different sites along the Muddy River Warm Springs area. Sites were restricted to the upper 6 km of the stream network within the thermally suitable range of *M. coriacea* (26 to 32 °C) (Scoppettone et al. 1998). Sites were selected to maximize coverage over thermal and spatial gradients. In summer 2008, organisms were collected from four intensively sampled sites. Organisms collected included green filamentous algae, epilithon, crustose benthic biofilm, coarse benthic organic material (CBOM), fine benthic organic material (FBOM), aquatic vascular macrophytes, herbaceous plants, tree leaves, benthic invertebrates, and fish. We define epilithon as photosynthetic diatoms and other algae on submerged rocks in the stream bed and crustose benthic biofilm as a matrix of bacteria, algae, fungi, and protozoa growing on rocks at the water line (Lowe and LaLiberte 2006, Stream Biofilm Research Group 2010). In summer 2009, six sites were intensively sampled and 14 sites were less intensively sampled for basic food web components. Less-intensive sampling included green filamentous algae, benthic invertebrates, and fish. Basic habitat characteristics were also recorded for sampling sites such as stream dimensions, substrate, and % canopy cover.

Green filamentous algae and crustose benthic biofilm were scraped from rocks from the stream channel. Epilithon was scrubbed and washed from rocks from within the stream channel. CBOM and FBOM were collected from riffle and pool stream

habitats. In riffle habitats, samples were taken using a 500- μm mesh kicknet and a small garden rake. In pool habitat, samples were collected by firmly placing a pipe 22 cm in diameter against the streambed, stirring inside with steel rebar, and scooping out suspended sediment. FBOM (< 1 mm) was sieved through 1-mm mesh and CBOM (> 1 mm) was left on top; both were collected. Stream-conditioned (decaying) aquatic vascular macrophytes, herbaceous plant material, and tree leaves were collected by hand from the stream. Benthic macroinvertebrates were sampled using a 500 μm mesh kicknet and a small garden rake (Bilby et al. 1996, Wallace et al. 2006, Mulholland et al. 2008). Fish were captured with minnow traps. Three adults and three juveniles of each species were retained except *M. coriacea*. Most *M. coriacea* were sampled by caudal clip. Four *M. coriacea* were sacrificed during the study to compare whole body stable isotope composition to caudal clip isotope composition (Hanisch et al. 2009). These samples were placed in labeled Whirl-Paks™ and frozen immediately.

Samples were thawed in a laboratory. Benthic macroinvertebrates were sorted to order. Snail shells and fish stomachs and intestines were removed prior to isotope analysis. Periphyton and FBOM were filtered on Whatman™ GF/F glass fiber filters. All samples were oven dried at 60 °C for > 24 hours and placed in a desiccator for two hours. Filters were placed in 60-cc labeled glass vials and sealed. All other samples were homogenized with a mortar and pestle then packed in glass vials. Very small samples were packaged whole. Equipment for handling samples and the work space

were wiped down with 95% ethanol between each sample to minimize the risk of contamination (Chaloner et al. 2002).

Stable isotope samples were analyzed by the Ecosystems Center, Marine Biological Laboratory stable isotope facility in Woods Hole, Massachusetts for spectral analysis. Animal, plant, and sediment samples were packed into tin capsules and weighed to +/- 0.01 milligrams. The stable carbon (^{13}C) and nitrogen (^{15}N) isotope compositions were determined using a Europa ANCA-SL elemental analyzer - gas chromatograph preparation system attached to a continuous-flow Europa 20-20 gas source stable isotope ratio mass spectrometer (M. Otter pers. comm.).

Food web diagrams were constructed from the results of this analysis (Hershey et al. 2006). First, Welch modified two-sample *t*-tests were used to test for differences between the same types or organisms over the two sampling years ($n > 10$; *p*-value cutoff 0.05). To test the hypothesis that *M. coriacea* depend on a food web supported by autochthonous production, carbon and nitrogen stable isotope ratios were plotted for specific groups. Trophic groups of interest were primary producers, terrestrial plants, invertebrates, and fish. Means and ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were compared for each group.

To test the hypothesis that *M. coriacea* exhibit stable isotope signatures that reflect secondary consumption of the most abundant drifting invertebrate orders within their range we used drift biomass data from StSaviour et al. (2011). In this study, we ranked the dry mass (g) per 24 hours of drifting macroinvertebrate orders from 6 sites where *M. coriacea* are present. Drifting macroinvertebrates were captured with 250-

μm drift nets, sorted to order, dried at 60°C for > 24 hrs, and weighed to determine drift rates (biomass per unit time and per unit volume). Weights were converted to dry mass per 24 -hr period by the following equation: $(\text{DM}/\text{Q}_{\text{net}}/t)/24$ where DM = dry mass, Q_{net} = discharge through the drift net, and t = net set time (hours) (adapted from (Smock 2006). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ means and 95% confidence intervals of specific invertebrate orders and *M. coriacea* were displayed in a table and graphically. Mean values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the three most abundant invertebrate orders by biomass were compared to those of *M. coriacea*.

To test the hypothesis that isotopic signatures of primary producers change along the stream course, distances (m) were measured from each sampling site to its primary source along the stream course using ArcGIS™ software version 9.3. Linear regressions were then used to test the relationship between the distance to the source spring and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of primary producers. Primary producers included filamentous algae, epilithon, and aquatic vascular plants. Crustose benthic biofilm was excluded from this analysis because it was a matrix of heterotrophic and autotrophic organisms with a highly enriched $\delta^{13}\text{C}$ signature. Linear fit scatter plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of primary producers as functions of distance in meters to the source spring were constructed to visually display regression results.

Lipid corrections of $\delta^{13}\text{C}$ were unnecessary for these samples. Plant material had a relatively low percent carbon ratio with low variance (mean % carbon = 28.75, 95% confidence interval 26.62 to 30.88%). Carbon to nitrogen ratios (C:N) were similar between primary consumers (invertebrates) and end members (fish). There

was also low variation in C:N ratios between these two groups (mean invertebrate C:N = 5.98, 95% confidence interval 5.78 to 6.18; mean fish C:N = 4.6, 95% confidence interval 4.45 to 4.75). Lipid corrections have been recommended when C:N ratios of aquatic animals exceed 3.5 (Post 2007); our samples averaged a C:N ratio of 4.5. When we examined the effect of a mathematical lipid correction, results were unchanged.

Mixing models were not used for this analysis for several reasons. When using the mixing model approach, ideally there are distinct differences in $\delta^{13}\text{C}$ signatures between autochthonous and allochthonous sources (Fry 1991). This was not the case in the Muddy River Warm Springs. Unexplained variability in algal $\delta^{13}\text{C}$ signatures between sites and lack of true epilithic algal endpoints created uncertainty in mixing model results (Finlay 2001). Moreover, mixing models are difficult to apply to omnivorous organisms because their prey items differ greatly in C:N ratios (Post 2002).

Results

There was no statistically significant difference between 2008 and 2009 isotopic signatures for any major groups of organisms sampled (two-sided p -value > 0.07 from a Welch modified two-sample t -test for all groups with a sample size > 10). Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from both years are pooled for the following analysis.

The Muddy River food web, including Moapa dace, was supported primarily by allochthonous inputs at the time of sampling. Mean $\delta^{13}\text{C}$ value of primary producers was -19.44‰ (95% confidence interval: -21.42 to -17.46‰). Compared to

allochthonous inputs, these values were more enriched and had a much wider range (Fig. 2 and Table 2). Mean $\delta^{13}\text{C}$ value of allochthonous inputs was -27.48‰ (95% confidence interval: -28.07 to -26.89‰). Primary consumers (macroinvertebrates) reflected isotopic signatures consistent with consumption of allochthonous material (mean macroinvertebrate $\delta^{13}\text{C} = -28.22\text{‰}$, 95% confidence interval: -28.90 to -27.53‰). $\delta^{15}\text{N}$ signatures increased 1.60‰ from allochthonous material to macroinvertebrates compared to no apparent increase from primary producers to macroinvertebrates. Mesquite (*Prosopis* spp.) had a particularly depleted $\delta^{15}\text{N}$ signature (mean = -1.35‰ , 95% confidence interval: -1.93 to -0.77‰)

Muddy River fishes, including Moapa dace, exhibited isotopic signatures consistent with secondary consumption of macroinvertebrates (mean fish $\delta^{13}\text{C} = -26.66\text{‰}$, 95% confidence interval: -27.14 to -26.18‰). There is a 1.6‰ shift in the $\delta^{13}\text{C}$ signature and a 4.3‰ shift in the $\delta^{15}\text{N}$ signature from Muddy River macroinvertebrates to fishes.

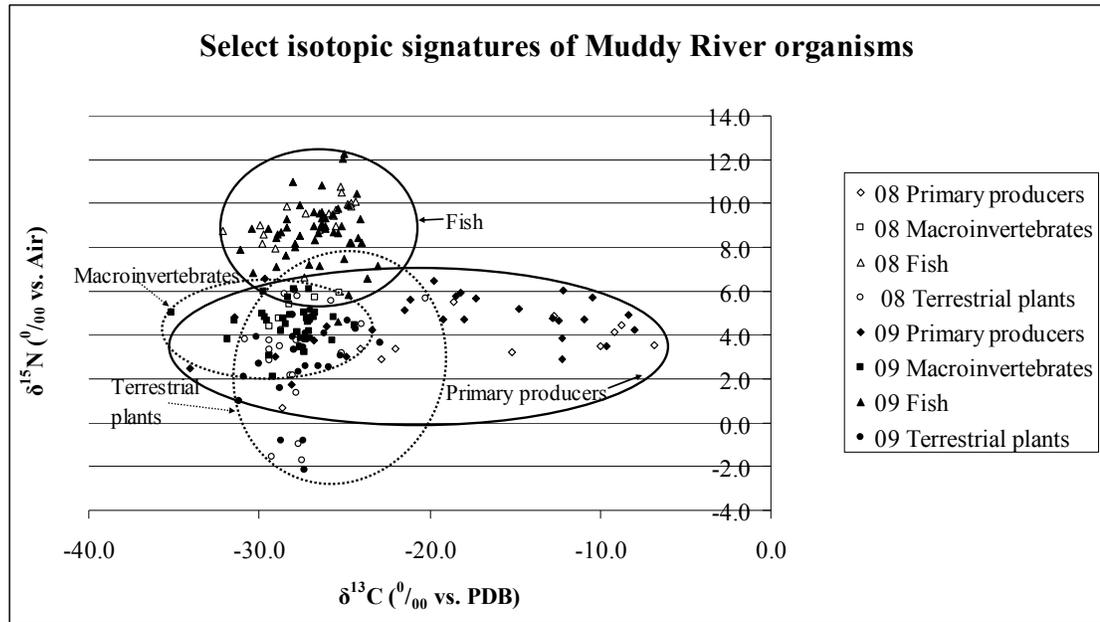


Fig. 2. Food web diagram of Muddy River Warm Springs organisms.

Table 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Means and 95% confidence intervals for Muddy River Warm Springs aquatic organisms.

Category	n	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
		mean	95%CI lower	95%CI upper	mean	95%CI lower	95%CI upper
Primary producers	53	-19.44	-21.42	-17.46	4.09	3.72	4.46
-Filamentous algae	25	-21.67	-24.32	-19.03	4.42	3.79	5.04
-Epilithon	10	-20.85	-23.8	-17.9	4.01	3.25	4.77
-Crustose benthic biofilm	10	-9.46	-10.56	-8.36	4.27	3.77	4.77
-Aquatic vascular plants	8	-23.19	-28.46	-17.91	2.93	1.9	3.95
Allochthonous sources	48	-27.48	-28.07	-26.89	3.04	2.44	3.63
-Semi-aquatic plants	15	-27.52	-28.33	-26.71	4.07	3.26	4.89
-Terrestrial plants	33	-27.47	-28.27	-26.66	2.57	1.82	3.32
CPOM	11	-22.79	-25.5	-20.08	4.01	3.31	4.71
FPOM	11	-12.06	-15.6	-8.53	5.06	4.23	5.89
All macroinvertebrates	35	-28.22	-28.9	-27.53	4.6	4.3	4.91
-Herbivorous macroinvertebrates	29	-28.19	-28.98	-27.39	4.47	4.13	4.81
-Omnivorous macroinvertebrates	6	-28.37	-30.04	-26.69	5.23	4.58	5.89
All fish	69	-26.66	-27.14	-26.18	8.85	8.54	9.16
-C. baileyi	11	-28.35	-29.72	-26.99	9.26	8.59	9.94
-G. affinis	5	-24.84	-25.39	-24.29	10.24	8	12.48
-M. coriacea	29	-25.94	-26.51	-25.37	8.7	8.16	9.25
-O. aureus	2	-27.65	-53.7	-1.6	9	3.92	14.08
-P. mexicana	22	-27.07	-27.99	-26.16	8.5	8.08	8.92

In 2008, Trichoptera, Neotaenioglossa (*Pyrgulopsis*), and Coleoptera were the three most abundant orders of drifting macroinvertebrates in terms of biomass per unit time at sites where Moapa dace occurred. In 2009, the most abundant orders were Neotaenioglossa, Coleoptera, and Hemiptera, respectively (Table 3).

Table 3. Ranked biomass of orders at sites where *M. coriacea* are present (2008 and 2009) (from StSaviour et al. 2011).

Order	2008				Order	2009			
	DM(g)/ 24hr	% of total	DM(g)/ 100m3	% of total		DM(g)/ 24hr	% of total	DM(g)/ 100m3	% of total
Trichoptera	2.8433	32.06	1.6737	15.83	Neotaenioglossa	1.9615	24.28	1.5016	17.32
Neotaenioglossa	2.1484	24.22	1.6160	15.28	Coleoptera	1.7402	21.54	1.6823	19.40
Coleoptera	0.6827	7.70	1.5355	14.52	Hemiptera	1.5697	19.43	2.3341	26.91
Lepidoptera	0.6459	7.28	0.7860	7.43	Diptera	1.0161	12.58	1.3738	15.84
Ephemeroptera	0.5896	6.65	0.3986	3.77	Trichoptera	0.8206	10.16	0.7126	8.22
Basommatophora	0.3368	3.80	0.2932	2.77	Ephemeroptera	0.5295	6.55	0.4076	4.70
Diptera	0.3285	3.70	0.7887	7.46	Odonata	0.1236	1.53	0.0722	0.83
Hymenoptera	0.3283	3.70	0.5741	5.43	Amphipoda	0.1125	1.39	0.0678	0.78
Amphipoda	0.3175	3.58	0.3754	3.55	Lepidoptera	0.0723	0.89	0.2605	3.00
Hemiptera	0.2829	3.19	1.1614	10.98	Hymenoptera	0.0602	0.75	0.1164	1.34
Araneae	0.1566	1.77	0.4493	4.25	Acari	0.0579	0.72	0.0396	0.46
Ostracoda	0.1406	1.59	0.7034	6.65	Ostracoda	0.0084	0.10	0.0808	0.93
Odonata	0.0318	0.36	0.1072	1.01	Thysanoptera	0.0057	0.07	0.0124	0.14
Acari	0.0289	0.33	0.1057	1.00	Araneae	0.0000	0.00	0.0104	0.12
Thysanoptera	0.0073	0.08	0.0057	0.05	Basommatophora	0.0000	0.00	0.0000	0.00

Stable isotope analyses were not conducted for all orders. However, isotopic signatures of Moapa dace were consistent with consumption of the most abundant orders in the drift (Coleoptera, Hemiptera, Neotaenioglossa, and Trichoptera). There was 2.3‰ shift in $\delta^{13}\text{C}$ signatures and a 4.1‰ shift in $\delta^{15}\text{N}$ signatures from Muddy River macroinvertebrates to Moapa dace (Fig. 3 and Table 4). The $\delta^{13}\text{C}$ mean value of tested macroinvertebrates was -28.2‰ (95% confidence interval: -28.9 to -27.5‰); their $\delta^{15}\text{N}$ mean value was 4.6‰ (95% confidence interval: 4.3 to 4.9‰). The mean $\delta^{13}\text{C}$ value of *M. coriacea* was -25.9‰ (95% confidence interval: -26.5 to -25.4‰); whereas their $\delta^{15}\text{N}$ mean value was 8.7‰ (95% confidence interval: 8.2 to 9.3‰).

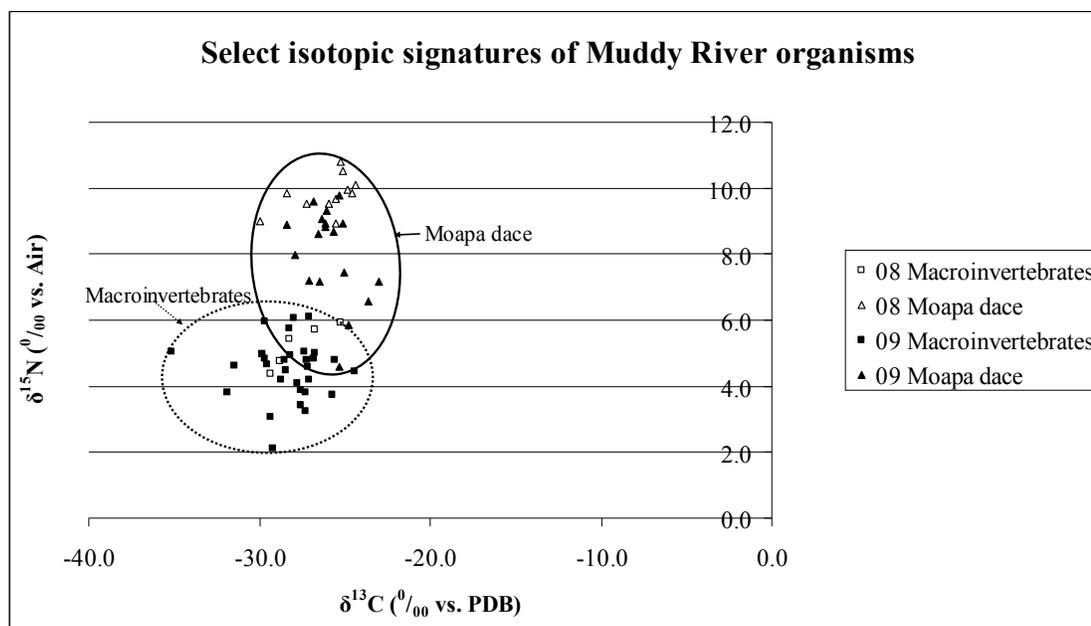


Fig 3. Food web diagram of *M. coriacea* and their prey.

Table 4. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Means and 95% confidence intervals of *M. coriacea* and their prey.

Category	n	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
		$\delta^{13}\text{C}$	95%CI	95%CI	$\delta^{15}\text{N}$	95%CI	95%CI
		mean	lower	upper	mean	lower	upper
All macroinvertebrates 2008	5	-27.72	-29.78	-25.66	5.22	4.42	6.02
-Ephemeroptera 2008	2	-28.10	-44.62	-11.58	5.05	-3.21	13.31
-Trichoptera 2008	3	-27.47	-32.17	-22.76	5.33	3.84	6.83
All macroinvertebrates 2009	30	-28.30	-29.07	-27.53	4.50	4.16	4.16
-Diptera 2009	2	-27.10	-61.41	7.21	4.70	0.89	8.51
-Coleoptera Elmidae 2009	19	-27.85	-28.52	-27.17	4.37	3.91	4.83
-Ephemeroptera 2009	5	-29.92	-34.31	-25.53	4.30	3.32	5.28
-Neotaenioglossa <i>Pyrgulopsis</i> 2009	1	-28.30	NA	NA	5.70	NA	NA
-Trichoptera 2009	3	-29.27	-30.72	-27.81	5.13	3.25	7.01
<i>M. coriacea</i> 2008	11	-26.05	-27.25	-24.86	9.79	9.41	10.18
<i>M. coriacea</i> 2009	18	-25.87	-26.54	-25.20	8.04	7.34	8.73

$\delta^{13}\text{C}$ signatures of primary producers (excluding crustose benthic biofilm) increased by 1.1‰ per 1000 m from the spring source (two-sided p -value = 0.0557 from an F -test; $R^2 = 0.12$)(Fig. 4). Primary producer $\delta^{15}\text{N}$ signatures also had a positive relationship with distance from their source; 0.3‰ per 1000 m from the spring source (two-sided p -value = 0.0476 from an F -test, $R^2 = 0.12$) (Fig. 4).

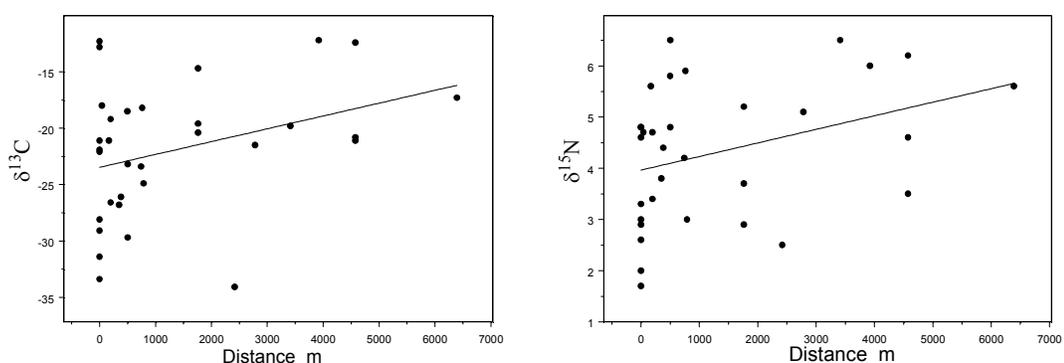


Fig. 4 Linear fit scatterplots of primary producers (excluding epilithon) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures as a function of distance in meters from their primary source.

Discussion

The importance of allochthonous sources in this spring system was not consistent with our hypothesis that autochthonous sources would provide the majority of the food base in these open streams. Many aquatic systems are supported by autochthonous sources to a greater degree than allochthonous sources due to the labile nature of algae. Algae have fewer high molecular weight structural compounds and lower C:N ratios than allochthonous sources. Even though autochthonous sources are frequently relatively scarce compare to allochthonous sources, they often play a more

significant role in supporting aquatic food webs due to their high quality (McCutchan and Lewis 2002, Hamilton et al. 2004, Allan and Castillo 2007). Exceptions are where lack of sunlight limits photosynthesis systems such as heavily forested headwater streams or limnocrenes (Finlay 2001, Wilson and Blinn 2007). Light-limitation probably is not the explanation for this result in the Muddy River Warm Springs area. Canopy cover ranges from 0 to 90% with a mean of 37.4% at sites where stable isotope samples were collected.

Allochthonous inputs could be of greater importance in this system due to variation in the amount or quality of terrestrial inputs versus algal production. Variation in the abundance of particular functional feeding groups could also strongly influence the way that carbon is cycled in an aquatic system. If detritivores were more abundant and available as prey for fish, then terrestrial inputs would be more important in the food web (Finlay 2001). Detailed diet analyses of fish and invertebrates could shed more light on this possibility. Allochthonous inputs provided 60% of the annual energy budget at Devil's Hole, NV, a thermal limnocrene (Wilson and Blinn 2007). In contrast, removal of non-native riparian tamarisk at Jack Rabbit Spring, Ash Meadows National Wildlife refuge, NV, resulted in an increase in primary production and population increase of native herbivorous pupfish (Kennedy et al. 2005). Mesquite may play a particularly important role in the Muddy River Warm Springs food web. We found that $\delta^{15}\text{N}$ enrichment from mesquite to macroinvertebrates (6.2‰) was greater than from other terrestrial sources (1.6‰).

Mesquite may be more labile than other allochthonous sources because it is associated with nitrogen-fixing bacteria (Virginia et al. 1984).

Invertebrate $\delta^{13}\text{C}$ values were much closer to those of terrestrial inputs than of autochthonous sources. Invertebrates exhibited the expected 2 to 3‰ increase in $\delta^{15}\text{N}$ values from terrestrial nutrient sources (Peterson and Fry 1987, Fry 1991). No such increase was evident from primary producers to invertebrates. Curiously, even the herbivorous invertebrates that we tested showed no trophic enrichment from algae. It is possible that these herbivores consumed different plants than were represented in our samples as a result of their feeding behavior or feeding location. There was greater trophic enrichment from the invertebrates we analyzed to the fish (4 to 5‰), perhaps because fish are consuming some predatory invertebrates and larval fish with higher $\delta^{15}\text{N}$ values. These food resources would be critical for *M. coriacea*, which must maximize their energetic intake due to their highly active behavior and the physiological demands of the thermal spring environment.

Wide variation was observed in the $\delta^{13}\text{C}$ values of the primary producers ranging from -34.1 to -6.9‰. This wide range of values can be attributed to the amount of inorganic carbon available, the source $\delta^{13}\text{C}$ value of that inorganic carbon, and how much a particular organism fractionates (Rounick and James 1984, Allan and Castillo 2007, Doctor et al. 2008). We assume that a given group of similar organisms, such as green filamentous algae, have similar metabolic pathways so the taxa of algal species sampled should not cause large variation in $\delta^{13}\text{C}$ values. The

amount of available carbon affects fractionation in these groups by influencing the amount of light carbon available for use (Finlay 2001).

Deep groundwater entering the springs is supersaturated with CO₂ from the carbonate aquifer, which is abundantly available to algae at the springheads (Bassett 2003). With little limitation of dissolved inorganic carbon (DIC), algae will use more ¹²C than ¹³C and fractionate to a greater degree than algae with less DIC available to them (Finlay 2001). Studies in artificial stream channels demonstrated that algae are less selective for lighter carbon isotopes under lower abundances of DIC (Hecky and Hesslein 1995, Trudeau and Rasmussen 2003). Algae in close proximity to a ground water source would have access to more DIC and exhibit more depleted δ¹³C values. However, since excess CO₂ diffuses rapidly as it comes into equilibrium with the atmosphere nearby algae may not have near as much DIC available to them. Aside from the main springs, there are numerous ground water seeps throughout the system that could be contributing water supersaturated in CO₂ and to the highly variable algal δ¹³C values.

Variation in velocities at sampling sites could be partially responsible for variation in δ¹³C of primary producers. Filamentous algae in lower velocity zones and epilithic algae in the boundary layer have been shown to exhibit enriched δ¹³C values compared to filamentous algae in higher velocity areas because the DIC supply is not replenished as quickly to algae in low velocity zones. With all other environmental variables held constant, algae in the lowest velocity areas had δ¹³C isotopic ratios as

high as -16.7‰, whereas the highest velocity areas had ratios as low as -28.1‰ (Trudeau and Rasmussen 2003).

$\delta^{13}\text{C}$ values at the spring sources also determine the isotope values of primary producers. Factors that can affect the isotope values in the spring sources are carbonates in ground water, high diffusion rates of CO_2 , heterotrophic respiration, and enrichment of the DIC pool by autotrophic fractionation (Rounick and James 1984, Allan and Castillo 2007). $\delta^{13}\text{C}$ value of DIC at the springheads of the Muddy River Warm Springs was measured to be -6‰ (Bassett 2003). With an average depletion factor of -21‰, this is a reasonable source value for the observed $\delta^{13}\text{C}$ range of primary producers (Rounick and Winterbourn 1986). However, there is no reason to expect much variability in $\delta^{13}\text{C}$ value of groundwater in the study area, so this does not explain the wide variation $\delta^{13}\text{C}$ values of primary producers.

Another possible mechanism explaining wide ranging algal $\delta^{13}\text{C}$ values is that microbial respiration in the soil along the stream banks could be contributing depleted DIC to the water (Rounick and James 1984, Allan and Castillo 2007). Respiration could be quite patchy in distribution with much more occurring in depositional zones of the stream. Desert soils in this region typically have soil gas CO_2 $\delta^{13}\text{C}$ values of -22‰ (Bassett 2003). This depleted CO_2 soil gas readily dissolves into water and could be used by algae in the benthic zone. A solute tracer experiment was conducted to examine the influence of groundwater nitrogen and dissolved organic carbon (DOC) in Grapevine Canyon Stream, in the Mojave Desert. Groundwater DOC concentration varied little among source sites with an average concentration of 2.96 mg C L⁻¹.

However, DOC concentration was strikingly different among stream sites, ranging from 1.77 mg C L⁻¹ to 7.44 mg C L⁻¹. This suggests a strong interaction between surface chemistry and groundwater sources (Jones 2002).

Factors affecting the amount and source value of DIC available to primary producers likely contributed to the observed pattern of downstream $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ enrichment in the Muddy River Warm Springs system. Less DIC would be available downstream from the source springs because CO_2 is degassed from the water as it comes into equilibrium with atmospheric CO_2 concentrations. ^{12}C diffuses faster than ^{13}C , so there is a reduction in the total amount of CO_2 and fractionation occurring as you move downstream (Choi et al. 1998, Doctor et al. 2008). DIC $\delta^{13}\text{C}$ isotopic ratios decreased by 3 to 5‰ 500 m from the source at a spring fed stream on Sleepers River Research Watershed, Vermont (Doctor et al. 2008). At Jack Rabbit Spring, Ash Meadows, Nevada, algal $\delta^{13}\text{C}$ increased 2.8‰ per 1000 m and $\delta^{15}\text{N}$ increased 0.8‰ per 1000 m (Kennedy et al. 2005).

In a downstream direction, increasing biomass of algae and aquatic macrophytes take up DIC through photosynthesis, reducing the overall DIC pool and fractionate carbon (Farquhar et al. 1982, Talling 1976). In a study that measured pH as a surrogate for DIC, phytoplankton in Esthwaite Lake, Cumbria, UK, consumed between 50% and 62% of available DIC during photosynthesis. In closed vessel experiments, algae depleted nearly all available DIC, with pH values reaching 10.4 (Talling 1976).

The pattern of downstream algal $\delta^{15}\text{N}$ enrichment is more difficult to interpret, but some of the same physical processes are likely at work. The amount of total nitrogen should not decrease, but perhaps increase in a down stream direction due to an increase in the number of living organisms. Nitrogen source values could become more enriched in a downstream direction due to more light nitrogen being used by organisms over the stream course enriching the nitrate and ammonium pool. This pool could also become enriched by a shift in trophic status where more omnivores and predators cycle through the system in lower reaches excreting wastes of prey consumed at higher trophic levels. Another possibility is nitrogen pollution. Livestock grazing was prevalent in lower reaches of the study area until 2008. Agricultural land use has been linked to elevated $\delta^{15}\text{N}$ values of stream biota (Vander Zanden et al. 2005).

Conclusion

Carbon and nitrogen stable isotope analysis indicates that the Muddy River Warm Springs system is primarily supported by allochthonous inputs. Riparian grasses and shrubs in the upper reaches may provide a major portion of the food base, and riparian forests of native trees (e.g. mesquite (*Prosopis* spp.) and ash (*Fraxinus velutina*)) and non-native trees (e.g. fan palm (*Washingtonia filifera*) and tamarisk (*Tamarix* spp.) may shade the lower reaches and provide large inputs of organic matter. Habitat restoration efforts that focus on establishing high-nutrient and labile forms of native stream-side vegetation would likely enhance food web productivity and food availability for *M. coriacea*. These results also suggest that *M. coriacea* are

feeding generalists, because no specific prey items that we tested seemed to be of greater importance to them.

Patterns of downstream enrichment in algal C and N indicate changes in carbon availability and nutrient cycling over the stream course and have implications for interpreting stable isotope food webs of spring systems. Investigators should have an understanding of how isotopic signatures change over the gradient of the system being studied when interpreting stable isotope results of spring systems.

Acknowledgements

Thanks to Dr. Stan Gregory (Department of Fisheries and Wildlife, Oregon State University) for guidance and moral support. Thanks to Dr. Matt Mesa (USGS, Western Fisheries Research Center, Columbia River Research Lab) for supporting this work through a research assistantship. Thanks to Chris Dixon (USGS) and Cailin Doyle (SNWA) for field assistance and good company. Thanks to Erin Boyle (USFWS) for GIS assistance.

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CHAPTER 3: MACROINVERTEBRATE DRIFT AVAILABILITY FOR MOAPA
DACE (*MOAPA CORIACEA*) IN THE MUDDY RIVER WARM SPRINGS AREA,
MOAPA, NEVADA

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ABSTRACT.-- Desert spring systems are associated with a high degree of endemism and endangered species. Understanding ecological limitations on these species and how these systems will be affected by anthropogenic water withdrawals is critical to their conservation. We investigated food as a potential limitation to endangered, thermophilic, drift-feeding Moapa dace (*Moapa coriacea*) by quantifying macroinvertebrate drift throughout their current and historic range within the Muddy River Warm Springs. This spring system naturally cools in a downstream direction. Drift was collected, sorted to order, and quantified as (dry) biomass per unit time and per unit volume in 2008 and 2009. Linear regression and non-metric multi-dimensional scaling (NMS) were used to examine the relationship of total drift biomass and temperature, specific macroinvertebrate order biomass and temperature, and associations between these orders and Moapa dace abundance. Lastly, we explored habitat characteristics associated with Moapa dace and their prey. In 2008 and 2009, total drift biomass/time was negatively correlated with temperature and positively correlated with discharge. In 2009, total biomass/volume had a negative linear relationship with temperature and a positive linear relationship with discharge, though these relationships were absent in 2008. Most macroinvertebrate orders were negatively associated with temperature in both years. The only positive associations with temperature were orders Lepidoptera and Neotaenioglossa in 2008. Moapa dace were associated with high temperatures, low stream discharge, shallow depth, and low drift biomass both years. They were positively associated with thermally tolerant Lepidoptera and Neotaenioglossa in 2008 and no orders in 2009. Macroinvertebrate

drift may be greater in cooler, downstream reaches because temperatures in those reaches are favorable to more taxa, there is more cumulative benthic area contributing to production, and there are fewer drift feeding insectivores. Moapa dace are excluded from these productive reaches by invasive species and fish barriers. Maintaining spring flows, eradicating non-natives, and restoring system connectivity will likely benefit Moapa dace and other Muddy River Warm Springs endemics.

Key words: Drift, Moapa dace, *Moapa coriacea*, thermophilic, endemic, temperature, stream discharge

Like many desert aquatic systems, the headwater Warm Springs region of the Muddy River near the town of Moapa, Clark County, Nevada, hosts several endemic species (Meffe and Vrijenhoek 1988). These include the critically endangered cyprinid minnow, the Moapa dace (*Moapa coriacea*) (Scoppettone et al. 1998). There are also five thermophilic endemic invertebrates: two snails (*Tryonia clathrata*) and (*Pyrgulopsis avernalis*), a water bug (*Limnocois moapensis*), and two elmids (*Microcyloepus moapensis*) and (*Stenelmis caiida moapa*) (Scoppettone et al. 1994).

Moapa dace co-exist in the Muddy River Warm Springs with the much more abundant, native, benthic feeding fish, the White River springfish (*Crenichthys baileyi*) (Scoppettone et al. 2005). Moapa dace were first collected in 1938 and described by Hubbs and Miller (1948). They have had federal protected status since 1967 (U.S. Fish and Wildlife Service 2002). There is a great deal of interest in

conserving this species. In this study, we examine food availability as a potential limiting factor on this population.

Stream invertebrates that become dislodged from the benthos or purposely enter the water column remain suspended for a time and are carried downstream. Organisms and debris suspended in the water column are termed drift. Fish that feed on drifting organisms are called drift feeders. Moapa dace are primarily insectivorous drift feeders (Scopettone et al. 1992, Scopettone et al. 1994). For many species, drift feeding is more energetically favorable than benthic feeding. Of similar species that feed on drift and benthos, drift feeders have repeatedly been shown to have much higher prey mass in their stomachs. This difference can be an order of magnitude or more (Nakano et al. 1999, Nakano and Furukawa-Tanaka 1994). Drift feeding fish can wait for food to be delivered to them rather than expending energy actively searching and digging through the benthos. The best sites for drift feeding are where a fish can hold with minimum energy expenditure adjacent to a concentration of stream flow. For example, a riffle that is funneled by large boulders or logs into a lower velocity pool is an ideal location. The concentration of the flow can effectively increase the field of view for a drift feeder by funneling drift from a larger area through a smaller high-velocity slot (Grant and Noakes 1987).

The purpose of this study is to understand patterns of macroinvertebrate drift availability to Moapa dace throughout the Muddy River Warm Springs system and relationships between drift and temperature. We quantified drift and characterized habitat throughout the potential range of Moapa dace. By identifying and quantifying

invertebrate communities across the thermal regime, we explored the implications of potential decreased discharge as a result of regional water table lowering or expansion of non-native palm riparian forests, both of which could lower the extent of warm water available for Muddy River Warm Springs thermophilic endemics (Lamberti and Resh 1983, Scopettone et al. 2006). We tested the following hypotheses: 1) Drift biomass are greater in reaches with warmer temperature and thus greatest near the thermal spring sources. 2) Neotaenioglossa, Hemiptera, and Lepidoptera are represented by a large proportion of thermally tolerant genera in the Muddy River system and are likely to be associated with the warmest temperatures. Conversely, Ephemeroptera and Trichoptera are less thermally tolerant and are associated with cooler temperatures. 3) Abundance of Moapa dace is greater in reaches with greater drift biomass and thermally tolerant drifting invertebrate taxa. Additionally, we explored associations between 17 other habitat variables and abundance of Moapa dace and their important food resources.

METHODS

Study Site

The Muddy River Warm Springs emanate from a deep Paleozoic carbonate aquifer. There are six spring areas within a 2-km radius with a cumulative discharge of 1.1 m³/s and little flow variation (Scopettone et al. 1992). The Moapa Warm Springs area is located in the Mojave Desert at 545 m elevation and 36°42'40.93"N 114°42'52.00"W latitude longitude. Average maximum and minimum air temperatures are 43.1 °C and 23.3 °C, respectively, in July and 16 °C and 0 °C in

December. The Moapa area receives an average of 11 cm of precipitation annually (Community Environmental Monitoring Program 1999), most of which falls in summer monsoon events.

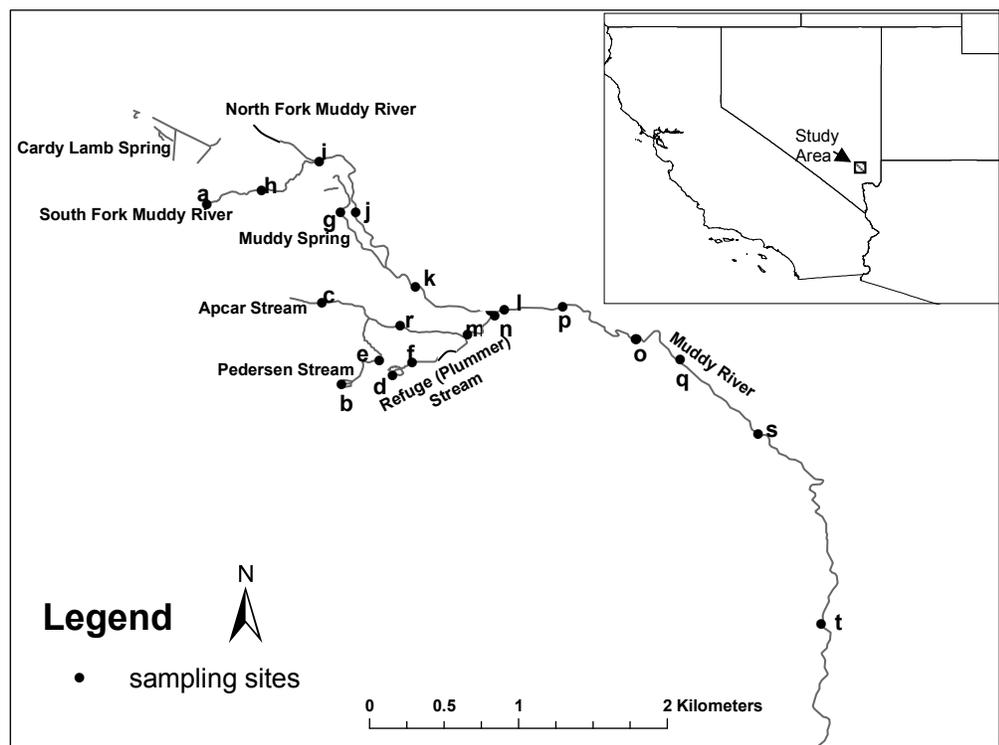


Fig.1: Upper Muddy River, Warm Springs Area, Clark County, NV, USA. Sampling sites are marked by solid circles and described individually in Table 1.

Table 1: Sample site habitat characteristics. Substrate type codes: (0) Silt/clay (< 0.059 mm), (1) Sand (0.6-1 mm), (2) Gravel (2-15 mm), (3) Pebble (16-63 mm), (4) Cobble (64-256 mm), (5) Boulder (>256 mm), (6) Bedrock. Riparian species: P= Palm (*Washingtonia filifera*), T= Tamarisk (*Tamarix* spp.), A =Ash (*Fraxinus velutina*), M= Mesquite (*Prosopis* spp.), AW= Arrowweed (*Pluchea sericea*), C= Cattail (*Typha latifolia*), W = Willow (*Salix* spp.), G= Grass (*Sporobolus airoides*), WP= Water Pimpernell (*Samolis* spp.), O= Other

Site Code	Avg temp (°C)	Q(m ³ /s)	Habitat Unit type	Avg. Width (m)	Max depth (cm)	Mean depth (cm)	Dominant Substrate	% Embededness	% Over-head cover	Riparian Species I
a	31.73	0.0945	Run	2.4	67	40	0	10	60	P, T, M, C
b	31.33	0.0059	Riffle	0.9	13	12	3	20	0	AW, O
c	31.27	0.0405	Run	0.9	20	18	1	50	75	P
d	30.88	0.0604	Riffle	1	25	18	3	20	40	M, W, C, AW
e	30.99	0.0991	Run	1.6	28	22	3	20	30	A, C, WP
f	30.76	0.0925	Run	3.5	50	35	0	10	20	P, C
g	30.92	0.1579	Run	3.3	52	30	2	10	60	P, T
h	30.23	0.0936	Riffle	1.6	38	34	3	25	15	C, AW
i	29.70	0.2936	Riffle	4.5	38	16	2	30	60	P
j	29.29	0.4223	Riffle	5	40	30	2	20	60	P, T
k	29.19	0.6406	Glide	11.4	43	25	4	30	0	P, T, C, M
l	28.61	1.0045	Run	7.9	55	30	1	25	10	AW, W, T, O
m	28.44	0.2596	Run	2.3	60	60	1	20	90	A
n	27.71	0.2877	Glide	4.75	30	20	1	10	70	T, G, O
o	27.64	0.8711	Run	8	60	40	1	5	15	M, AW, T
p	28.20	0.7446	Riffle	8	65	40	1	25	10	T, AW, O
q	27.62	0.9062	Run	6	60	50	3	30	50	A, P, AW
r	27.72	0.1130	Riffle	1.25	12	12	3	40	75	A, O
s	27.17	0.9337	Riffle	4.9	46	29	3	90	20	P, AW, M, A
t	28.77	0.7163	Run	4	120	90	4	30	10	T, W, O

Temperatures of spring sources range from 31.0 to 32.0 °C with little annual variation (< 2.2 °C), and dissolved oxygen ranges from 4.1 to 6.2 mg/L (Scoppettone 1993). Moapa dace are active fish that spend much of their time in relatively high velocity currents (up to 55 cm/s focal point velocity) (Scoppettone et al. 1992). Considering this environment and behavior, energetic costs for maintaining feeding positions would be very high.

Land use practices and invasive species have been detrimental to Moapa dace and other native fauna. Springs were diverted to swimming pools, homes, and businesses. Intensive livestock grazing and two large fires have denuded riparian vegetation and destabilized banks. Introduced palm trees (*Washingtonia filifera*), tamarisk (*Tamarix spp.*), cattails (*Typha latifolia*), and aquarium grass (*Valisineria spp.*) have replaced much of the native vegetation. Non-native vertebrate introductions have included short-finned molly (*Peocilia mexicana*), mosquito fish (*Gambusia affinis*), blue tilapia (*Oreochromis aureus*), and spiny soft-shelled turtles (*Apalone spinifera*). These changes have caused declines in native fish populations (Deacon and Bradley 1972, Sada and Herbst 1999, Scoppettone 1993, Scoppettone et al. 2005).

Groundwater extraction for urban development threatens to reduce spring discharge, by reducing hydraulic head from the deep carbonate aquifer, a common problem in populated arid regions (Patten et al. 2007). A reduction in spring discharge would likely lead directly to a reduction in overall aquatic habitat and in thermally suitable habitat for Moapa thermophilic endemics (Scoppettone et al. 2006). Changes

of 3 °C to 4 °C can cause significant changes in the composition of invertebrate communities (Lamberti and Resh 1985).

Initial conservation efforts in the Muddy River Warm Springs area were targeted at land and water acquisition. The 47 ha Moapa Valley National Wildlife Refuge (MVNWR) was established in 1979 (U.S. Fish and Wildlife Service 2010). In 2007, the Southern Nevada Water Authority (SNWA) purchased the 477 ha Warm Springs Natural Area directly downstream of the MVNWR (Southern Nevada Water Authority 2009). There has been extensive habitat restoration occurring on both properties. Many organizations have been restoring native vegetation and removing invasive plants. Nevada Department of Wildlife has reclaimed sections of stream with rotenone treatments. Barriers have been constructed to keep blue tilapia out of remaining refugia for Moapa dace (Heinrich 1999).

Sample collection

Drift was collected once each summer from 20 sampling sites within the Muddy River Warm Springs area in 2008 and 2009. Sites were located in the upper 6 km of the spring network, the extent of thermally suitable habitat for Moapa dace (26 to 32 °C) (Scoppettone et al. 1998). Sites were selected to represent an even distribution of thermal and spatial gradients. Hobo™ temperature loggers were maintained at each site from April, 2008 through the duration of the study.

A Wildco™ drift net with 250 µm mesh size and 30 X 45 cm opening was staked into the stream bed at each sampling site for 45 min or until net began to clog. Drift nets were set in water approximately 20 cm deep with a velocity of 0.3 m/s,

comparable to average focal depth (15 – 113 cm) and velocity (0 – 55 cm/s) of Moapa dace (Scopettone et al. 1992). Each drift sample was placed into a 0.5 L Nalgene™ bottle and preserved with a 70% ethanol solution. Drift samples were sorted and invertebrates identified to order. Each invertebrate sample was dried for > 24 hours at 60 °C and in a desiccator for > 2 hours. Invertebrate samples were weighed to nearest 0.0001 g to obtain a dry mass (DM) for each order per site and year. Stream discharge and velocity at the drift net opening were measured at each sampling site using a SonTek™ acoustic Doppler velocimeter (ADV) (Smock 2006).

Habitat was characterized for 15-m stream segments at each sample site. Stream segments were first characterized by habitat unit: riffle, run, pool, or glide. In addition to temperature and discharge, net set time, depth at sampling location, mean and maximum depth, average width, substrate size and embeddedness, percent overhead cover, percent large and small wood, and riparian plant species were also recorded.

US Fish and Wildlife service biannual intensive snorkel survey data provided measures of abundance of Moapa dace for the study area. The entire study area was snorkeled in February and August each year. Counts of Moapa dace, but not other, more-abundant species, were recorded for each designated stream reach. There were 17 snorkel survey stream reaches ranging in length from 65 to 5000 m and in discharge from 0.006 to 1.000 m³/s.

Data reduction and analyses

Data consisted of DM of 20 orders from 20 sites; 2008 and 2009 were examined separately for all analyses. To quantify macroinvertebrate drift biomass per unit time, DM were converted to DM per 24 hour period by the following equation: $(DM/Q_{net}/t)*24$ where DM = dry mass, Q_{net} = the proportion of total discharge through the drift net, and t = net set time (hr) (adapted from (Smock 2006). Discharge differed by two orders of magnitude among sites. To account for differences in discharge, DM were standardized with the following equation: $(DM*100)/(t*Q_{net}*60)$ to yield a DM per 100 m³. The end result was four data matrices: 2008 mass/ time, 2009 mass/ time, 2008 mass/ volume, and 2009 mass/ volume. Each matrix contained site discharge measurements and average temperatures. To understand the number of food items encountered by drift-feeders, we examined drift density as counts (CT) of drifting macroinvertebrates/ time and / volume for both years. We then calculated the effect of drift consumption by dace on drift abundance with the equation [(natural consumption rate per 15 min * number of Moapa dace at a site) / (number of invertebrates passing a site per 15 min)]. In this equation we used an average maximum of six Moapa dace at a site (author's unpublished data) and natural consumption rate from a feeding behavior experiment (StSaviour and Gregory 2011).

One 2009 site sample was lost during shipping and had to be excluded from the 2009 data matrices. Four uncommon orders were removed from all data sets to improve normality and because they contributed less than 2% of biomass to the drift. Total biomass/ volume data was normal and met the assumptions of the parametric

statistics used. Normality of total biomass/ time was outside of the acceptable range of parametric statistics, but was much improved with the natural log transformation, so these data were natural log transformed for linear regressions.

Preliminary investigations indicated that discharge was a significant contributor to patterns observed in invertebrate and fish distribution, so it was included in final analyses. We investigated the relationship of total site drift biomass as a function of temperature and stream discharge using simple and multiple linear regression in the software package Splus™ version 8.0 (Martin 2008).

Nonmetric multidimensional scaling (NMS) (Kruskal 1964) was used to examine the relationships of specific orders with temperature and other environmental variables. Because dry masses of individual orders consisted of very low numbers (< 1) and many zeros and because back-transformation was unnecessary from NMS results, the generalized log transformation was used on these data. Generalized log transformations tend to preserve the original magnitude of the data and results in values of zero when the original value was zero. The generalized log transformation was applied with the equation: $b_{ij} = \log(x_{ij} + d) - c$. In this equation x_{ij} = the original value in row i and column j of the data matrix, b_{ij} = the adjusted value that replaces x_{ij} , c = order of magnitude constant = $\text{Int}(\log(\text{Min}(x)))$, and d = decimal constant = $\log^{-1}(c)$. $\text{Min}(x)$ is the smallest nonzero value in the data and $\text{Int}(x)$ is a function that truncates x to an integer by dropping the digits after the decimal point (McCune and Grace 2002). This transformation was applied to the main matrix and to the site biomass totals in the environmental matrix, substantially improving skewness,

kurtosis, and coefficient of variation (CV) (Table 2). NMS is robust to non-normal data but outliers will have a disproportional influence on the results. No site or order outliers greater than 2.5 standard deviations from the mean were detected after transformation.

Table 2: Summary statistics of site and order biomass/ volume data before and after the generalized log transformation.

	before transformation			after generalized log transformation			
	avg skewness	avg kurtosis	CV(%)	avg skewness	avg kurtosis	avg	CV(%)
2008							
site	3.22	10.79	68.28	0.37	-0.48		27.01
order	2.81	8.86	211.41	0.37	0.45		60.02
2009							
site	3.10	9.98	129.27	0.39	-0.58		41.45
order	2.73	8.60	212.77	0.56	0.75		67.90

NMS analysis was run in the software package PC-ORD version 6.0 (McCune and Medford 2009) on the 2008 and 2009 biomass/ volume. We investigated the relationship of orders and temperature using the biomass/ volume data because sites with higher temperatures had lower discharges and consequently lower biomass/ time. Fifty runs with real and randomized data were completed with an instability criterion of 0.00001. Sorensen distance was used for this analysis because it has a fixed maximum for sites that have no orders in common (McCune and Grace 2002).

The final solution was plotted and the point cloud was rotated to maximize the correlation of average temperature and axis 1 (McCune and Grace 2002). Pearson's correlation coefficient (r ; (Clarke and Ainsworth 1993) was calculated for each order to determine the strength of the relationship between temperature and ordination scores. NMS ordination overlays and Pearson's correlation coefficients were scrutinized to determine which orders were associated with the warmest temperatures and which other habitat variables explained their distribution. Coefficients of determination (r^2) cutoffs were set to 0.2 and Pearson's r cutoffs at 0.5. These levels were relevant to these data sets considering the number of axis, number of variables, and variance within (McCune and Grace 2002).

Snorkeling counts of Moapa dace per reach were converted to dace per 100 m of stream length to standardize counts among variable reach lengths. Drift biomass/ volume data were condensed in cases where several drift biomass sites fell into a single snorkel survey reach by calculating the mean of biomass estimates within the reach. Habitat variables that were insignificant in the previous NMS were thrown out.

Values for remaining habitat variables were averaged similarly to the biomass data. The result was a 2008 main matrix that contained 12 reaches and 16 orders and a 2008 environmental matrix that contained 12 reaches and 6 habitat variables. The 2009 matrices were similar but contained 11 reaches.

Generalized log-transformed biomasses and NMS were again used to test if Moapa dace are associated with greater drift abundance and thermally tolerant drifting macroinvertebrate orders. Joint plots and Pearson's correlation coefficients were examined to determine the degree of association between Moapa dace, and ordination scores of all drifting macroinvertebrates as well as specific thermophilic orders. Joint plots were also examined to see which habitat variables were associated with greater abundance of Moapa dace and their important food resources. The main and environmental matrices were then combined and linear regressions were used to examine the relationship between Moapa dace and total biomass, as well as the relationship between Moapa dace and thermophilic orders.

Results

Table 3: Ranked biomass of orders in the Muddy River Warm Springs (2008 and 2009).

2008					2009				
Order	DM(g)/ 24hr	% of total	DM(g)/ 100m3	% of total	Order	DM(g)/ 24hr	% of total	DM(g)/ 100m3	% of total
Trichoptera	2.8433	32.06	1.6737	15.83	Neotaenioglossa	1.9615	24.28	1.5016	17.32
Neotaenioglossa	2.1484	24.22	1.6160	15.28	Coleoptera	1.7402	21.54	1.6823	19.40
Coleoptera	0.6827	7.70	1.5355	14.52	Hemiptera	1.5697	19.43	2.3341	26.91
Lepidoptera	0.6459	7.28	0.7860	7.43	Diptera	1.0161	12.58	1.3738	15.84
Ephemeroptera	0.5896	6.65	0.3986	3.77	Trichoptera	0.8206	10.16	0.7126	8.22
Basommatophora	0.3368	3.80	0.2932	2.77	Ephemeroptera	0.5295	6.55	0.4076	4.70
Diptera	0.3285	3.70	0.7887	7.46	Odonata	0.1236	1.53	0.0722	0.83
Hymenoptera	0.3283	3.70	0.5741	5.43	Amphipoda	0.1125	1.39	0.0678	0.78
Amphipoda	0.3175	3.58	0.3754	3.55	Lepidoptera	0.0723	0.89	0.2605	3.00
Hemiptera	0.2829	3.19	1.1614	10.98	Hymenoptera	0.0602	0.75	0.1164	1.34
Araneae	0.1566	1.77	0.4493	4.25	Acari	0.0579	0.72	0.0396	0.46
Ostracoda	0.1406	1.59	0.7034	6.65	Ostracoda	0.0084	0.10	0.0808	0.93
Odonata	0.0318	0.36	0.1072	1.01	Thysanoptera	0.0057	0.07	0.0124	0.14
Acari	0.0289	0.33	0.1057	1.00	Araneae	0.0000	0.00	0.0104	0.12
Thysanoptera	0.0073	0.08	0.0057	0.05	Basommatophora	0.0000	0.00	0.0000	0.00

In 2008 and 2009 the natural log of site biomass/ time totals were significantly negatively correlated with temperature and positively correlated with discharge (Fig. 2, Table 4). Drift density was also negatively correlated with temperature in both years (Table 4). Because these relationships had opposing slopes, models that incorporated both temperature and discharge yielded insignificant results.

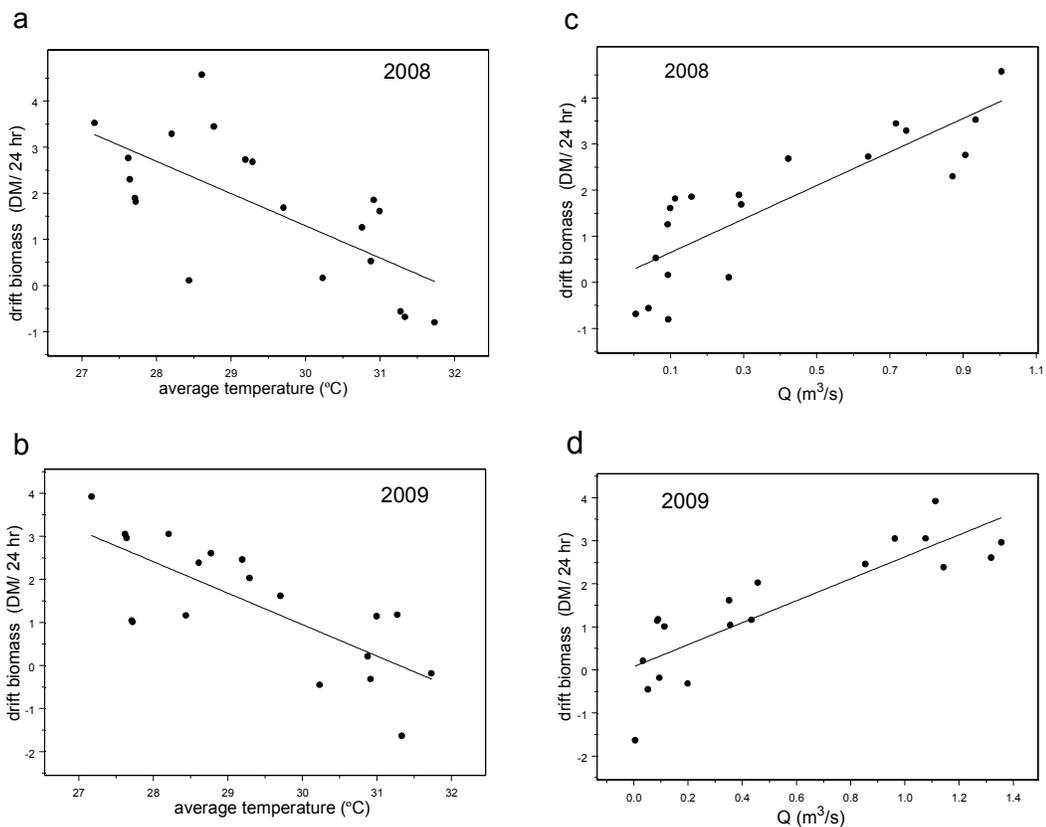


Fig. 2: Linear fit scatter plots of natural log back transformed drift biomass/ time (DM/ 24 hr) as a function of temperature (plots a and b) and discharge (Q) (plots c and d).

Table 4: Linear regression model outcomes for drift biomass and counts as a function of temperature and stream discharge. Total = total drift biomass at each site, ln = natural log transformed, avgTemp = average site temperature over the study period, avgQ.m3.s = the average stream discharge over the study period, and TotalCT = the total count of macroinvertebrates at each site.

Data set	Formula	p-value	R2	intercept	slope
2008DM-24hrs	lnTotal~avgTemp	0.0008	0.4704	22.26	-0.70
2008DM-24hrs	lnTotal~avgQ.m3.s	<0.0001	0.7046	0.28	3.64
2009DM-24hrs	lnTotal~avgTemp	0.0002	0.5704	22.87	-0.73
2009DM-24hrs	lnTotal~avgQ.m3.s	<0.0001	0.7334	0.08	2.55
2008DM-100m3water	Total~avgtemp	0.8890	0.0011	1.23	0.04
2008DM-100m3water	Total~Q.m3.s	0.6140	0.0144	2.11	0.57
2009DM-100m3water	Total~avgtemp	0.0651	0.1861	6.60	-0.18
2009DM-100m3water	Total ~ Q.m3.s.	0.0477	0.2112	1.01	0.59
2008CT-24hrs	TotalCt~avgTemp	0.0255	0.2479	1677954	-54389
2008CT-100m3water	TotalCt~avgTemp	0.7163	0.0075	-30884	1579
2009CT-24hrs	TotalCt~avgTemp	0.0018	0.4464	1110529	-35676
2009CT-100m3water	TotalCt~avgTemp	0.1821	0.1022	41690	-1136

In 2008 relationships between total site biomass/ volume and temperature or discharge were not statistically significant, but, these relationships were significant in 2009. Total biomass/ volume had a negative linear relationship with temperature and a positive linear relationship with discharge (Fig. 3, Table 4). Again, models that incorporated both temperature and discharge yielded insignificant results.

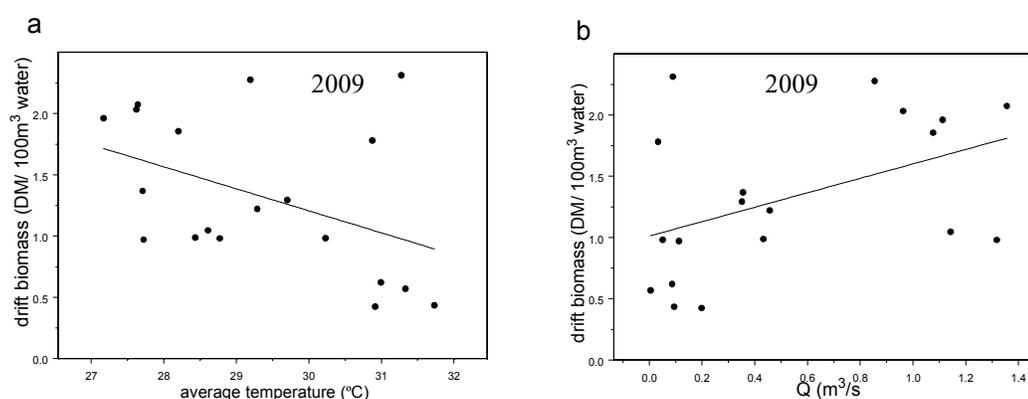


Fig. 3: Linear fit scatter plots of drift biomass/ volume (DM/ 100m³ water) as a function of temperature (plot a) and discharge (Q) (plot b).

To address the potential autocorrelation between stream discharge and temperature, we created a biplot of discharge and temperature and then repeated these analyses within a narrower range discharges and temperatures so that we could examine the effect of each separately (Fig. 4). Linear regressions of log total biomass/ time and biomass/ volume as functions of discharge and then temperature in 2008 and 2009 only yielded significant results for biomass/ time in 2009 (two-sided p -value = 0.0462 from an f -test). These results suggest that drift biomass was related to discharge but not closely related to temperature. However, sample size and statistical power were reduced when analyzing these narrower ranges.

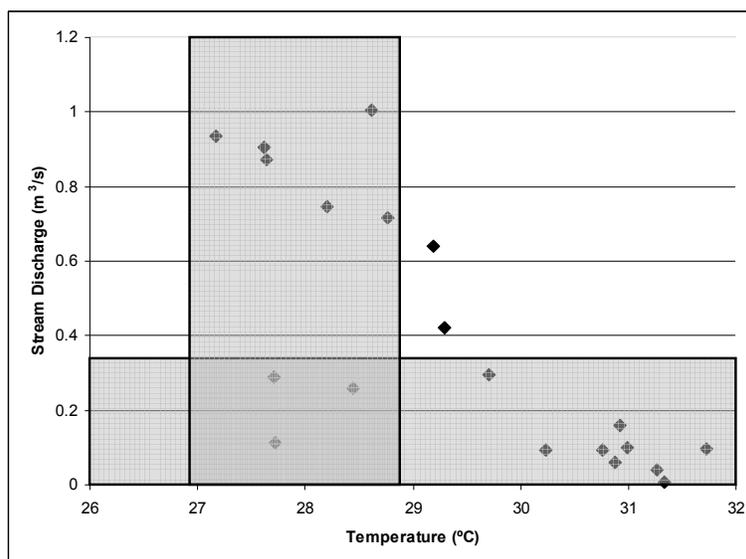


Fig. 4: Biplot of stream discharge vs. temperature. Sampling sites are marked by a “♦.” The narrower ranges of discharge and temperature that were analyzed for potential autocorrelation are highlighted with grey boxes.

In general, most orders were not associated with the warmest temperatures in 2008 and 2009. NMS ordinations converged on stable 2-dimensional solutions with the 2008 and 2009 data. The 2008 ordination required 101 iterations; it had a final stress of 10.29 and final instability of < 0.00001 . This 2-D solution accounts for 0.90 (cumulative r^2) of the variation in the original data set. The 2009 ordination required 59 iterations; it had a final stress of 10.44 and final instability of < 0.00001 . This 2-D solution accounts for 0.91 (cumulative r^2) of the variation in the original data set.

The 2008 overlay of total biomass on a gradient of community response to temperature is representative of the response of most orders to this axis (1) (Fig. 5). Ephemeroptera ($r = -0.612$) and Trichoptera ($r = -0.567$) were both significantly negatively associated with temperature in 2008. Ephemeroptera ($r = -0.846$) was

significantly negatively associated with temperature in 2009 but Trichoptera ($r = 0.021$) was not. The only orders that were positively associated with temperature were Lepidoptera ($r = 0.465$) and Neotaenioglossa ($r = 0.728$) in 2008. No orders were significantly positively associated with temperature in 2009.

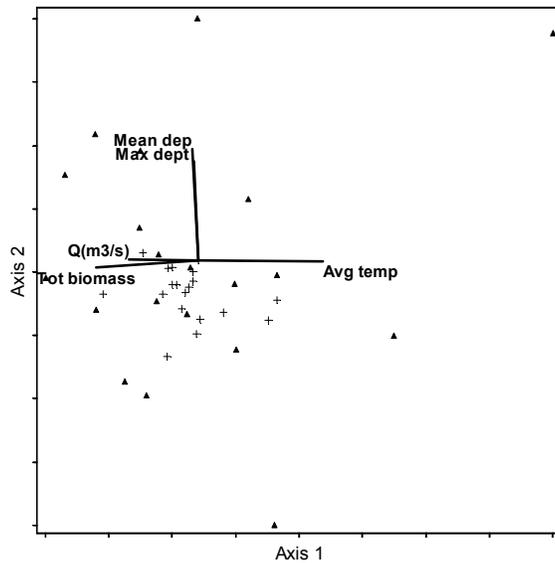


Fig. 5: NMS overlay of 2008 total drift biomass on a gradient of community response to temperature (axis 1). Sampling sites are marked with a ▲; macroinvertebrate order centroids are marked with a +.

Using the reduced data set that included the Moapa dace snorkel data, NMS ordinations converged on stable 2-dimensional solutions with the 2008 and 2009 data. The 2008 ordination required 41 iterations; it had a final stress of 9.18 and final instability of < 0.00001 . This 2-D solution accounts for 0.733 (cumulative r^2) of the variation in the original data set. The 2009 ordination required 51 iterations; it had a final stress of 10.68 and final instability of < 0.00001 . This 2-D solution accounts for 0.744 (cumulative r^2) of the variation in the original data set.

In 2008 and 2009 Moapa dace were associated with high temperatures, low stream discharge, shallow depth, and low drift biomass (r^2 cutoff value 0.2) (Fig. 5). No other habitat variables proved significant in explaining variation in community distribution. In 2008 they were positively associated with thermally tolerant orders Lepidoptera ($r = 0.608$) and Neotaenioglossa ($r = 0.858$). However in 2009 Moapa dace were not significantly associated with any orders (r^2 cutoff = 0.5) (Fig. 6).

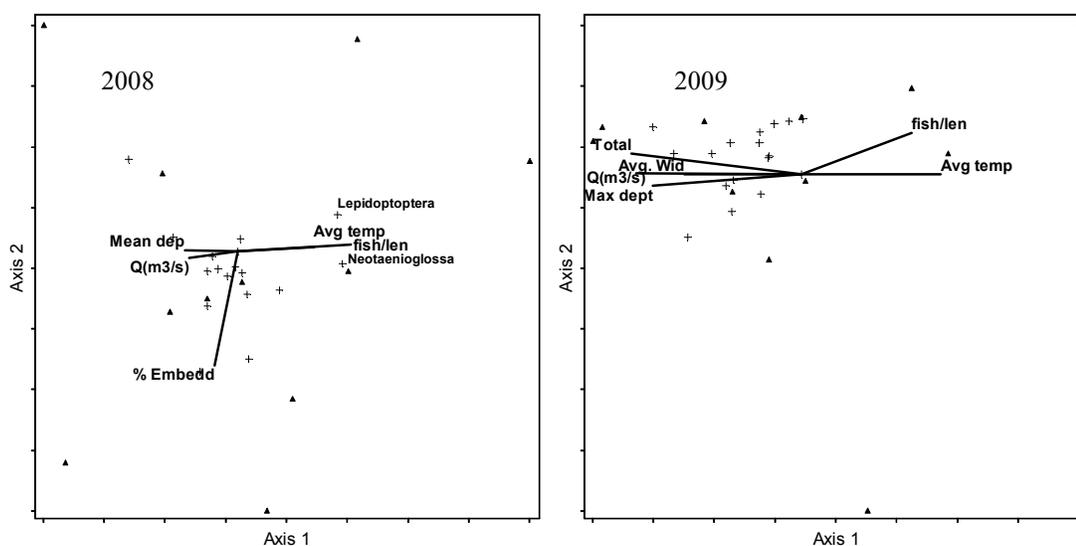


Fig. 6: 2008 and 2009 NMS jointplots of sample sites in order space. Sampling sites are marked with a ▲; macroinvertebrate order centroids are marked with a +.

“Fish/len” represents Moapa dace per 100 m of stream length.

Linear regression results indicate no significant relationship between generalized log-transformed fish/100 m of stream and generalized log total biomass/volume in 2008. There was a negative association between generalized log fish/100 m of stream and generalized log total biomass/ volume in 2009 (two-sided p -value = 0.067 from a t -test, $R^2 = 0.326$) (Fig. 7a). Generalized log fish/100 m of

stream was positively associated with generalized log Lepidoptera biomass/ volume in 2008 (two-sided p -value = 0.062 from a t -test, $R^2 = 0.307$) (Fig. 7b). The generalized log of fish/ 100 m of stream was not positively associated with any other orders in 2008 or 2009.

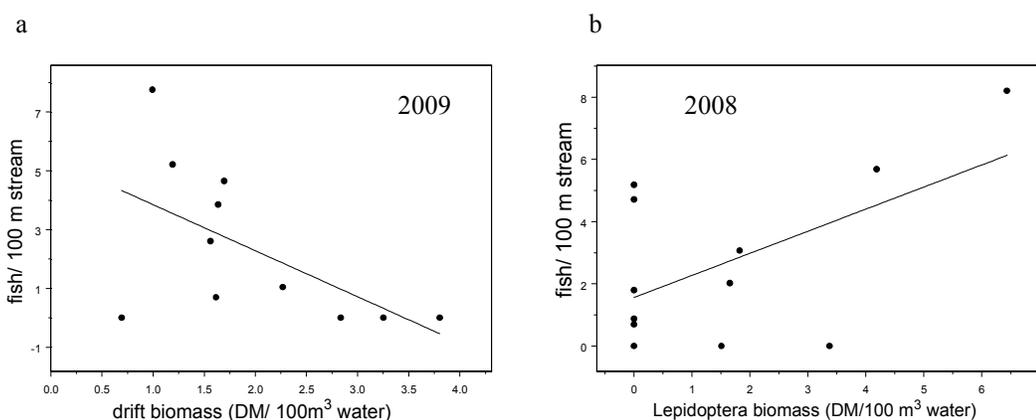


Fig 7: Linear fit scatter plots of Moapa dace/ 100 m of stream as a function of total drift biomass 2009 (plot a) and of drifting Lepidoptera biomass 2008 (plot b). Both axis have been generalized log transformed.

Discussion

Total drift biomass is greater in lower, cooler reaches where Moapa dace are not present. Physical forces associated with higher discharges may dislodge more invertebrates and increase drift in lower reaches. However, stream invertebrates should be adapted to the moderate velocities in these reaches. Relatively cooler temperatures (26-29 °C) may be more favorable to drifting invertebrates than warmer temperatures (30-32 °C). Over a range of similar temperatures, Lamberti and Resh (1985) found the highest densities of invertebrates at 34 °C but the highest biomass at

23 °C. We found a similar pattern between density and biomass at the Muddy River Warm Springs (Table 4). Because water temperature naturally decreases and discharge increases in a downstream direction, the two are inversely correlated in this spring system in contrast to most streams and rivers. Though drift biomass was corrected for stream flow, total drift biomass may be greater in lower reaches because there is greater benthic area available for invertebrate production. Downstream areas not only benefit from production within those reaches, but also from nutrients from upstream reaches (Vannote et al. 1980). Another possible mechanism for observed patterns in drift biomass could be predation. Drift feeding fish, such as Moapa dace, are relatively more abundant in upper reaches (Scoppettone et al. 1992) and could be depleting drift in these reaches (Kennedy et al. 2000, Leung et al. 2008). Assuming a maximum of six Moapa dace at a focal site, we found that they could consume 47% of the drift at the lower Pederson representative site. In a few cases as many as 30 Moapa dace have been recorded at a site (author's unpublished data). Considering these numbers, Moapa dace could have a substantial effect on drift abundance and limit their food supply at locations with high densities of dace. Macroinvertebrate density is usually negatively associated with increased predator abundance and positively associated with avoidance behavior (e.g. drifting at night) (Wooster and Sih 1995, Miyasaka and Nakano 1999, Huhta et al. 2000).

It is unlikely that Moapa dace, a drift feeding fish, is negatively associated with drift biomass because of habitat or resource selection. Ideal free distribution theory suggests that organisms should be distributed throughout their habitat in such a way to

match available resources (Fretwell and Lucas 1969). However, competition and travel impediments can alter this dynamic (Kennedy and Gray 1993). Range restriction of Moapa dace due to competition with and predation from other species and barriers to fish passage are probably responsible for much of the observed patterns (Sada and Herbst 1999, Scoppettone and Goodchild 2009). Introduction of non-native fish species has been implicated as a cause of decline of native desert fishes by means of direct predation, competition, and habitat alteration (Courtenay et al. 1985, Scoppettone et al. 1998, Scoppettone et al. 2005). Adult Moapa dace currently range from 40 to 90 mm in size (Scoppettone et al. 1992). Historically, much larger Moapa dace, up to 180 mm, existed in the main stem of the Muddy River, presumably a result of access to greater food availability (Scoppettone, pers. comm.).

Only temperature and stream discharge proved significant in explaining most of the variation of macroinvertebrate biomass and Moapa dace distribution. Warmer temperatures are associated with higher production (Lamberti and Resh 1985) and greater growth and metabolism of invertebrates (Lamberti and Resh 1983, Lamberti and Resh 1985, Vannote and Sweeney 1980). If temperature alone were driving invertebrate production in this system, then the greatest drift biomass should be found in upstream reaches. This was not observed in the Muddy River Warm Springs. If a wider range of temperatures were considered, it is plausible that an asymptotic relationship between biomass and temperature would emerge. Biomass may increase as temperature decreases and encompasses the preferred thermal range of more macroinvertebrates, but then it would decrease as the temperature became too cold to

support abundant and diverse invertebrate communities (Robin L. Vannote and Sweeney 1980). The Muddy River Warm Springs would be on the descending limb of this theoretical biomass to temperature curve.

The head waters of the Muddy River Warm Springs have nearly constant discharge, temperature, and water quality. Unlike most desert systems, including the lower Muddy River, the Warm Springs head water area is protected from large flash floods by a mesa that diverts the occasional monsoon floods to lower parts of the Muddy River (USGS 2010). The conditions at the lower Pederson flume are representative of where Moapa dace currently exist. Over the two year study period the average stream temperature at this site was 31.0 °C (minimum = 29.8 °C, maximum = 32.5 °C) (author's unpublished data); average stream discharge was 0.105 m³/s (minimum = 0.099 m³/s, maximum = 0.108 m³/s) (USGS 2010). Aquatic communities experiencing little environmental variability, such as those in the headwaters of the Muddy River Warm Springs, might have difficulty adapting to a sudden and permanent drop in discharge and temperature. Vannote and Sweeney (1980) state that thermal stability is important to maintaining a highly structured invertebrate community.

Conclusion

There is greater food availability in lower reaches of the Moapa dace's historic range. Aquatic invasives and fish passage barriers currently restrict the Moapa dace's use of many of these reaches. Access to those reaches will most likely lead to larger, healthier, more fecund individuals, and perhaps, an increase in the population size of

Moapa dace (Mann 1974, Mann and Mills 1985). In contrast, a reduction in drift, as a result of water loss, would likely lead to further population decline if drifting food is a limiting resource for Moapa dace. Reductions in spring discharge and associated drift levels may jeopardize the current population of ESA listed Moapa dace. Habitat restoration activities should consider the consequences of proposed actions on the productivity of drifting invertebrates. Efforts to eliminate non-native fish and other aquatic invasives and restore system connectivity are likely to benefit Moapa dace populations.

Acknowledgements

Many thanks to Dr. Stan Gregory (Department of Fisheries and Wildlife, Oregon State University) for guidance and moral support. Thanks to Dr. Matt Mesa (USGS, Western Fisheries Research Center, Columbia River Research Lab) for supporting this work through a research assistantship. Thanks to Chris Dixon (USGS) and Cailin Doyle (SNWA) for field assistance and good company. Thanks to Bill Gerth (OSU) for aid in identifying macroinvertebrates.

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CHAPTER 4: OBLIGATE DRIFT FEEDING BEHAVIOR OF MOAPA DACE

MOAPA CORIACEA: A DRIFT MANIPULATION EXPERIMENT

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Abstract.—Desert spring systems are associated with a high degree of endemism and endangered species. Understanding ecological limitations on these endangered fish species and how these ecosystems will be affected by anthropogenic water withdrawals is essential to their conservation. To investigate potential feeding behavior limitations of endangered, drift-feeding Moapa dace (*Moapa coriacea*), we experimentally manipulated food availability (0, 34, 64, 100, and 200% of the natural drift level) and quantified their feeding attempts, success, and consumption rates. We found that Moapa dace are obligate drift feeders, selecting drift 40 times more frequently than benthos. They did not adaptively shift foraging modes from drift to benthic when drift was reduced experimentally. Drift feeding rate increased in response to increasing drift. Mean number of drift feeding attempts per 15 minutes was 8.8 attempts higher at 100% and 16.0 attempts higher at 200% of the natural drift level than at the 0% drift level. Drift feeding success only increased from the 0% to the 64% drift level and did not change in the 100% and 200% levels. No relationship between aggression and food availability or fish size was detected. Moapa dace may share an interspecific foraging association with sympatric White River springfish (*Crenichthys baileyi*). Maintaining in-stream flows and restoring habitat to provide abundant drifting macroinvertebrates would likely aid in Moapa dace recovery.

Fish have adapted a wide array of feeding strategies that theoretically should maximize their energetic intake while minimizing expenditures (Hughes 1997). In most circumstances, insectivorous stream fish either feed on organisms that are

drifting in the water column or on the surface or feed on benthic organisms. For many species, drift feeding is more energetically favorable than benthic feeding. Among similar species that feed on drift and benthos, drift feeders often have higher prey mass in their stomachs. This difference can be an order of magnitude or more (Nakano et al. 1999; Nakano and Furukawa-Tanaka 1994). Drift feeding fish can wait for food to be delivered to them rather than expending energy actively searching and digging through the benthos. Focal sites for drift feeding are locations where a fish can maintain position with minimum energy expenditure adjacent to a concentration of stream flow. Concentration of the flow immediately at the head of a pool effectively increases the field of view by funneling drift from the larger area of the upstream riffle through a more narrow, high-velocity location (Grant and Noakes 1987). Because these types of sites are so desirable, dominant individuals aggressively defend focal sites (Nakano 1995; David et al. 2007; Hansen and Closs 2005).

Fish that feed on both drift and benthos may switch to benthic feeding when drift drops below an availability threshold. Dolly Varden, *Salvelinus malma*, adaptively switched feeding modes from drift to benthic foraging when drift was experimentally reduced in a Japanese stream, but sympatric white-spotted charr *S. leucomaenis* did not exhibit such a shift in feeding behavior under reduced-drift conditions. Ability to feed on drift or benthos is related to body morphology. Fish with more inferiorly-positioned mouths are better adapted to feed on benthos and more likely to do so when drift becomes depleted, as with Dolly Varden (Fausch et al. 1997; Nakano et al. 1999). Recently emerged brook charr, *S. fontinalis* exhibit natural

variation in body morphologies (McLaughlin and Grant 1994). Some have fusiform body shapes, narrow caudal peduncles, and large caudal fins, as expected for fish holding in higher velocities. Others take on characteristics of a benthic dweller, such as deeper bodies, thicker caudal peduncles, and smaller caudal fins. Fish with characteristics adapted for midwater were found in higher velocities than those with more benthic dwelling characteristics. These two morphs specialize in feeding in those parts of the water column for which they are best suited. Fusiform fish more often eat insects from the upper portion of the water column, whereas the benthic forms eat crustaceans from the lower portion of the water column (McLaughlin and Grant 1994; McLaughlin 2001). These fish have also been called “stayers” and “movers” respectively in other literature. Stayers are defined as ambush predators, who wait for their prey to come to them as drift feeders do. Movers actively search for their prey as many benthic feeders do (Grant and Noakes 1987; Holbrook and Schmitt 1989).

Environmental conditions can have profound effects on feeding behavior. Organisms inhabiting desert spring systems often experience extreme conditions of alkalinity, salinity, dissolved oxygen, and temperature, all of which cause physiological stress in fish. High temperatures limit gas solubility and thus dissolved oxygen content in water. Fish living in thermal systems are stressed by combined effects of elevated oxygen demand due to their high metabolic rates and a temperature-induced Bohr effect that interferes with hemoglobin function (Helfman et al. 2009a). The ability to adapt to extreme conditions reduces potential competition

with other species. Pupfish *Cyprinodontidae* are a well-studied family of extremophile fish that tolerate salinities greater than 90 ppt, dissolved oxygen levels as low as 0.13 mg/L, and temperatures as high as 45°C (Miller 1981). Metabolic studies of desert species indicate that most have increased metabolism with increasing temperature. Adaptations to low oxygen include high O₂ affinity hemoglobin and a greater proportion of cathodal blood hemoglobin which is resistant to Bohr effect. High salinity is managed by active transport across the basal-lateral gill membrane by the Na⁺ pump (Na⁺ -K⁺ ATPase) similarly to estuarine species (Hillyard 1981). These adaptations require an excess of energy, therefore food can be limiting in thermal springs (Constantz 1981). With increased metabolic rates in response to the thermal environment, there would be a greater need for food acquisition. The general expectation is fish will have increased feeding rates as temperature increases within their thermal preferenda (Costa-Dias and Lobón-Cerviá 2008). Food availability could be of critical importance in maintaining geographically isolated populations of thermophilic fishes.

Although environmental conditions are potentially challenging to the organisms of the Muddy River Warm Springs, the head springs themselves are characterized by a very stable temperature, flow regime, and water quality. Unlike most desert systems, including the lower Muddy River, the Warm Springs head water area is protected from large flash floods by a mesa that diverts the occasional monsoon floods to lower parts of the Muddy River (USGS 2010). Conditions at the lower Pederson flume are representative of where Moapa dace currently exist. Over the two

year study period the average stream temperature at this site was 31.0 °C (minimum = 29.8 °C, maximum = 32.5 °C) (author's unpublished data); average stream discharge was 0.105 m³/s (minimum = 0.099 m³/s, maximum = 0.108 m³/s) (USGS 2010).

In this study, we examine feeding behavior of an endangered cyprinid minnow, the Moapa dace *Moapa coriacea*, which exists in an extremely isolated and physiologically stressful environment. Moapa dace are primarily insectivorous drift feeders but occasionally feed on benthos (Scoppettone et al. 1992; Scoppettone et al. 1994). Moapa dace were first collected in 1938 and described by Hubbs and Miller (1948). They have had federal protected status since 1967 (U.S. Fish and Wildlife Service 2002) and occur primarily on the 47 ha Moapa Valley National Wildlife Refuge (MVNWR) and the 477 ha Warm Springs Natural Area directly downstream of the MVNWR (Southern Nevada Water Authority 2009). The biology and ecology of Moapa dace were examined by Scoppettone et al. (1992) in the Muddy River Warm Springs system. Moapa dace inhabit the spring sources at temperatures of 32 °C and extend downstream to larger streams where temperatures decrease to 26 °C at the lower limits of their distribution. Dissolved oxygen concentrations in the reaches occupied by dace ranged from 3.5 to 8.4 mg/L. Based on continuous presence of larval dace, Moapa dace are thought to spawn year-round at or near the springheads. They can reach sexual maturity at a length range of 40 to 45 mm which is achieved within their first year. Reproductive effort is asynchronous and continuous. Observed fecundity ranges from 60-772 but only a few eggs develop at a time. Moapa dace have been aged at 4+ years and become more fecund with increasing size (up to

90 mm currently). Larger adults occupy higher discharge areas away from the spring sources, which also tend to have cooler temperatures. Previous gut-contents analyses indicate a low biomass in general and an average composition of 75% macroinvertebrates and 25% plant material. Moapa dace populations have been documented as high as 2,800 but have decreased in recent years and were estimated to be 697 in 2010 (Scoppettone et al. 1992, USFWS unpublished data 2010).

Groundwater extraction for urban development threatens to reduce spring discharge, by reducing hydraulic head from the deep carbonate aquifer, a common problem in populated arid regions (Patten et al. 2007). A reduction in spring discharge will likely lead directly to a reduction in overall aquatic habitat and in thermally suitable habitat for Moapa thermophilic endemics (Scoppettone et al. 2006).

If spring discharges and aquatic habitats are reduced by groundwater extraction, abundance of drifting macroinvertebrates consumed by Moapa dace may be altered. We wanted to determine if Moapa dace would be able to adapt to a reduction in drift by shifting their feeding behavior. In this study, drift was experimentally manipulated and Moapa dace feeding behavior was observed to test following hypotheses: 1) Based on their morphology and ability to feed on drift and benthos, Moapa dace will adaptively shift from drift to benthic feeding under reduced drift abundance; 2) Moapa dace feeding increases and aggression decreases with greater drift abundance; 3) larger Moapa dace defend more effective drift-feeding territories, and therefore feed at a higher rate and more successfully than smaller Moapa dace.

Study Area

Moapa dace inhabit the headwater warm springs that feed the Muddy River, Clark County, Nevada. The springs emanate from a deep Paleozoic carbonate aquifer. There are six spring areas within a 2-km radius with a cumulative discharge of 1.1 m³/s and little flow variation (Scoppettone et al. 1992). The Moapa Warm Springs area is located in the Mojave Desert at 545 m elevation and 36°42'40.93"N 114°42'52.00"W latitude longitude. Average maximum and minimum air temperatures are 43.1 °C and 23.3 °C, respectively, in July and 16 °C and 0 °C in December. The Moapa area receives an average of 11 cm of precipitation annually (Community Environmental Monitoring Program 1999), most of which falls in summer monsoon events.

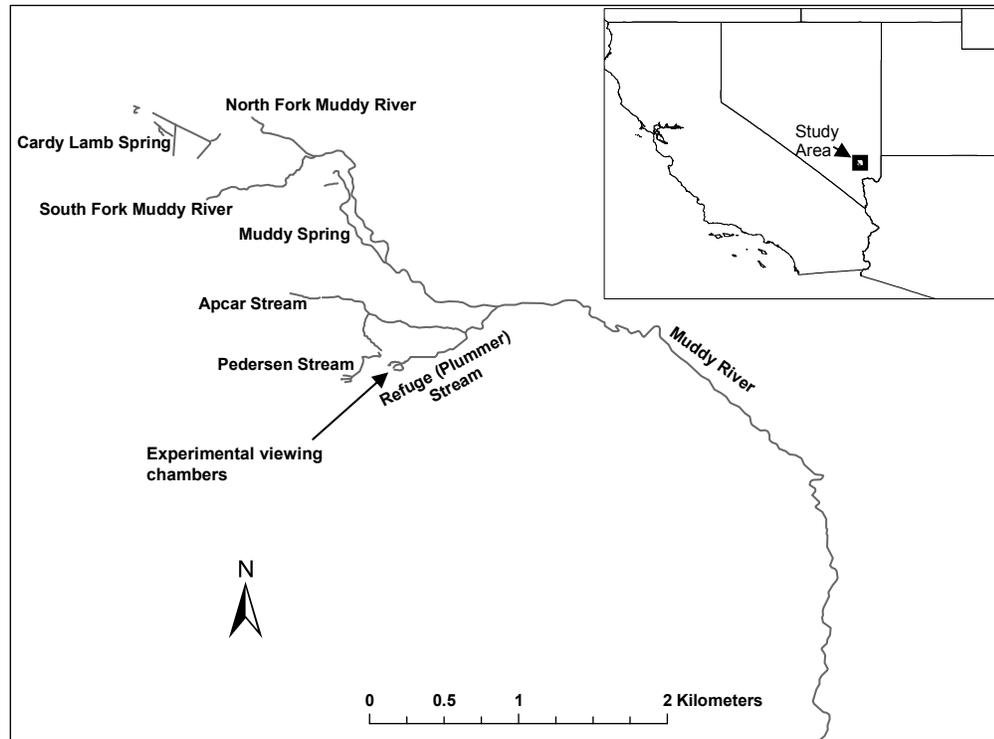


Figure 1.-- Upper Muddy River, Warm Springs Area, Clark County, NV, USA.

Temperatures of spring sources range from 31.0 to 32.0 °C with little annual variation (<2.2 °C), and dissolved oxygen ranges from 4.1 to 6.2 mg/L (Scoppettone 1993). Moapa dace are active fish that spend much of their time in relatively high velocity currents (up to 55 cm/s focal point velocity) (Scoppettone et al. 1992). Considering this environment and behavior, energetic costs for maintaining feeding positions would be very high. Moapa dace co-exist in the Muddy River Warm Springs with the much more abundant, native, benthic feeding fish, the White River springfish *Crenichthys baileyi*, hereafter termed springfish. The exotic, generalist, the short-finned molly *Peocilia mexicana* and small, exotic, predator, mosquito fish *Gambusia*

affinis are also present. Blue tilapia *Oreochromis aureus* exist below several fish passage barriers where they have displaced Moapa dace (Scopettone et al. 2005).

Methods

The drift manipulation experiment was conducted in May of 2009 in the “Plummer Stream,” at the Moapa Valley National Wildlife Refuge. Two viewing pools with windows built into one side of the natural stream were used as the feeding observation areas (Figures 2 and 4). Moapa dace were captured with minnow traps, weighed, measured, and marked by caudal clip. In preliminary trials with natural drift levels, fish resumed normal feeding behavior within 1 hr after capture, and variance in drift feeding stabilized at twelve 1-min observation periods. In a second preliminary trial, six Moapa dace were held with virtually no drift. Dace fed very little during this trial and it was suspended at four hours to prevent death of these endangered fish.



Figure 2.--Recording feeding observations through viewing windows



Figure 3.--Drift nets

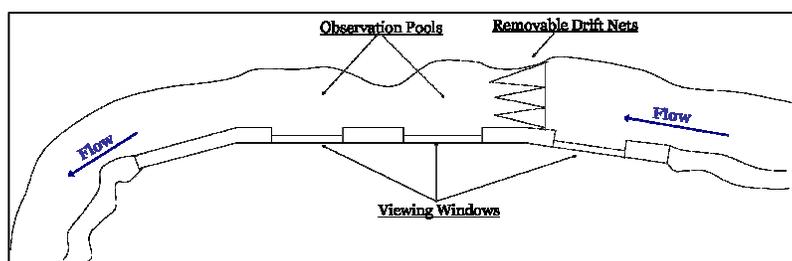


Figure 4.--Overview schematic of experimental design

During drift manipulation trials, three marked fish were placed into each of two observation pools and allowed to acclimate for at least 2 hr. Test subject fish were kept in their respective observation pools using semi rigid, plastic, 5-mm mesh “block nets”. Feeding behavior of individual Moapa dace was observed under five different drift treatment levels. The natural level of drift was considered to be 100%. Drift then was depleted to 64%, 34%, and 0% of the natural drift level using a series of three 250- μ m drift nets just upstream of the viewing windows (Figures 3 and 4). There was also a drift addition treatment of 200%, where drift collected during the 0%

treatment was periodically added over the observation period. Block nets were cleaned between each treatment. Each test subject fish was exposed to the five treatments over two days. The experimental sequence was repeated for 37 individual Moapa dace, 31 of which remained in the observation section for all five treatments.

For a single treatment, feeding behavior was observed for an individual fish on a rotating basis for 1 min until we had 15 observations for each of the six test subjects in the observation pools. Observations for a set of six fish were repeated for each treatment. For each feeding event, we noted the type of feeding (drift, benthic, or surface), success in a feeding attempt (capture of an item), whether they accepted or rejected the item, and the quadrant of the pool in which they fed. We also recorded aggressive interactions between co-occurring dace or springfish.

Data were initially reduced by removing observations on non-feeding behavior like time and spatial data. Surface feeding was extremely rare (< 1 % of all feeding) and was excluded from this analysis. Fish that did not complete all treatments also were excluded. Data were reduced additionally by summing feeding observations per fish and per treatment, representing total observations of each fish as a single number. The resulting data matrix consisted of treatment, fish number, fish length * six behavioral responses. The six behavioral responses were: total drift feeding attempts, proportion of successful drift feeding attempts to total drift feeding attempts, drift consumption (attempts * success), total benthic feeding attempts, proportion of successful benthic feeding attempts to total benthic feeding attempts, and aggressive interactions towards or from another fish.

Drift and benthic feeding attempts were square root transformed in order to meet the assumptions of the models used in this analysis. The square root transformation equalized and reduced variances; it also improved skewness (2.0 to 0.7) and kurtosis (6.9 to 0.6). The estimated means and confidence intervals of the square root of drift feeding attempts were back transformed for interpretation.

To confirm that Moapa dace are obligate drift feeders, first total drift and benthic feeding attempts were compared for each fish using a Welch modified two-sample *t*-test. To determine if Moapa dace can shift to benthic feeding under reduced drift conditions, the square root of drift feeding attempts, drift feeding successes, square root of drift consumption, square root of benthic feeding attempts, and benthic feeding successes were analyzed separately as functions of the drift treatment level. A linear mixed effects model with random effects grouped by fish and an analysis of variance (ANOVA) table was used to analyze these repeated measures data by using a blocking factor. Blocks were a single fish subjected to five treatments. The design is balanced because all fish included in the analyses were observed under all treatments. This model was used to test for among treatment heterogeneity in fish behavior after accounting for the variance of individual fish.

Linear mixed models do not produce a traditional R-squared statistic. A pseudo R-squared metric was calculated for each model to compare the amount of variance in the original dataset to the amount of variance in the model residuals and is represented by the equation $((\text{Total Sum of Squares} - \text{Residual Sum of Squares}) / \text{Total Sum of Squares})100\%$ (Ramsey and Schafer 2002; Singer 1998).

To determine if Moapa dace feeding is a function of drift availability, the same models were used with the addition of Tukey-Kramer multiple comparisons for drift feeding success as a function drift treatment level. We calculated the effect of drift consumption on drift abundance with the equation [(number of invertebrates passing a site per 15 min) - (natural consumption rate per 15 min * number of Moapa dace at a site)]. In this equation we used an average maximum of six Moapa dace at a site (author's unpublished data). To assess the relationship between aggression and drift availability, no formal statistical test was used due to a lack of independence between observations of aggressive behavior. Instead, all aggressive interactions were summed for each treatment to evaluate the overall trend in aggressive behavior as a function of drift availability.

To determine the relationship between Moapa dace feeding and fish size, a linear mixed effects model with random effects grouped by fish was again used to analyze this repeated measures experiment. Drift feeding attempts, drift feeding successes, and aggressive interactions were analyzed separately as functions of fish length. Total aggressive interactions per treatment and fish size were not formally tested but were investigated for trends with a scatterplot.

Results

Total mean drift feeding attempts differed significantly from total mean benthic feeding attempts (square root transformed; two-sided p -value < 0.0001 from a Welch modified two-sample t -test). Moapa dace fed on drift approximately 40 times more frequently than benthos (back square root transformed; mean drift feeding

attempts = 106.1 and mean benthic feeding attempts = 2.6 in 15 min; difference between means = 74.8, 95% confidence 54.8 to 98.0 (Fig. 5).

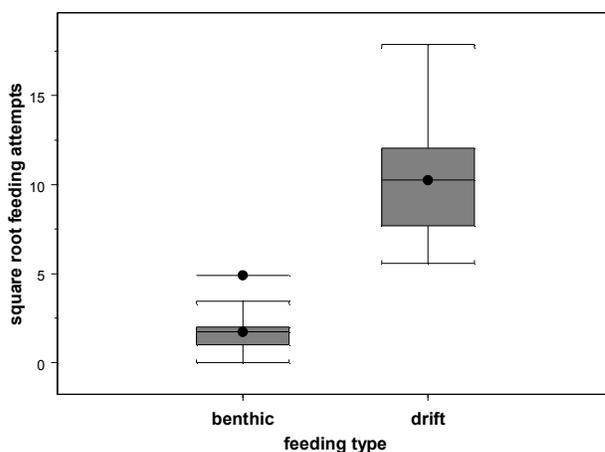


Figure 5.--Square root of total Moapa dace benthic and drift feeding attempts in 65 min at all drift treatment levels; whiskers represent 1.5*interquartile range.

Mean number of drift feeding attempts differed across the 5 different drift treatment levels (square root back-transformed; p -value < 0.0001; ANOVA F -test). Mean number of drift feeding attempts increased as drift level increased. Moapa dace mean drift feeding attempts per 15 min were 8.8 (95% confidence interval: 3.1 to 16.7) higher in the 100% drift treatment level than in the 0% level and 16.0 (95% confidence interval: 8.56 to 25.65) higher in the 200% level than in the 0% level (95% confidence interval: 8.6 to 25.7) (Fig. 6, Appendix 1). Drift treatment level accounted for 68.5% of the variation in the square root of drift feeding attempts.

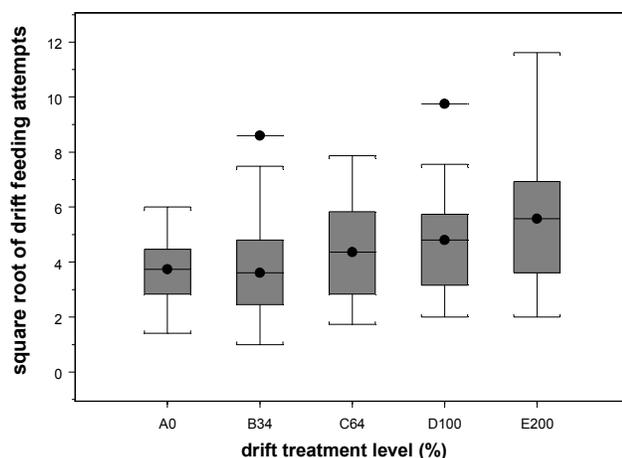


Figure 6.—The square root of Moapa dace drift feeding attempts per 15 min as a function of % natural drift available; whiskers represent 1.5*interquartile range.

Mean proportion of successful drift feeding across the 5 different drift treatment levels also differed significantly (p -value < 0.0001; ANOVA F -test). Mean proportion of successful drift feeding increased significantly from the 0% to the 64% drift treatment level and did not change in the 100% and 200% levels. Moapa dace were 24.0% (95% confidence interval: 15.8% to 32.3%) more successful in drift feeding at the 64% drift treatment level than the 0% level. They were only 16.1% (95% confidence interval: 7.9% to 24.4%) more successful in drift feeding at the 200% drift treatment level than the 0% level. 95% confidence intervals for multiple comparisons by the Tukey method indicated that difference in mean proportional drift feeding success between the 64% and 100% drift treatment levels ranged from -15.8% and 11.1%; between the 64% and 200% levels the range is -21.3% and 5.6%. Drift treatment level accounted for 47.3% of the variation in proportional drift feeding success (Fig. 7).

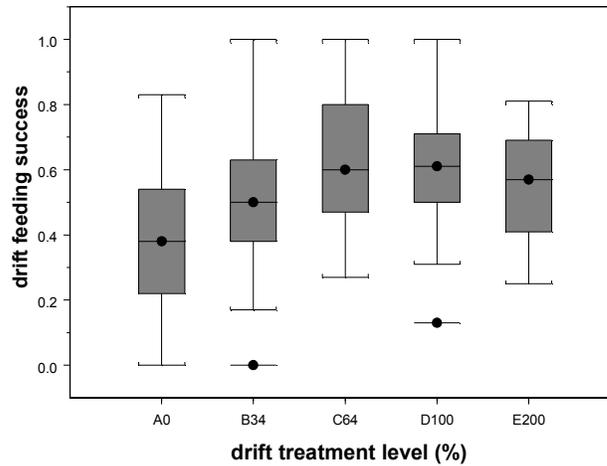


Figure 7.-- Moapa dace proportional success of drift feeding attempts per 15 min as a function of % natural drift available; whiskers represent 1.5*interquartile range.

Drift consumption also increased as drift level increased (square root transformed; p -value < 0.0001; ANOVA F -test). Moapa dace had 5.7 (95% confidence interval: 1.6 to 9.8) mean drift consumption events per 15 min at the 0% drift treatment level compared to 15.9 (95% confidence interval: 7.6 to 24.2) at the 100% level and 18.6 (95% confidence interval: 10.3 to 26.9) at the 200% level (Fig. 8). Drift treatment level accounted for 65.4% of the variation in the square root of drift consumption. At the lower Pederson representative site, we found that Moapa dace could consume 47% of available drift.

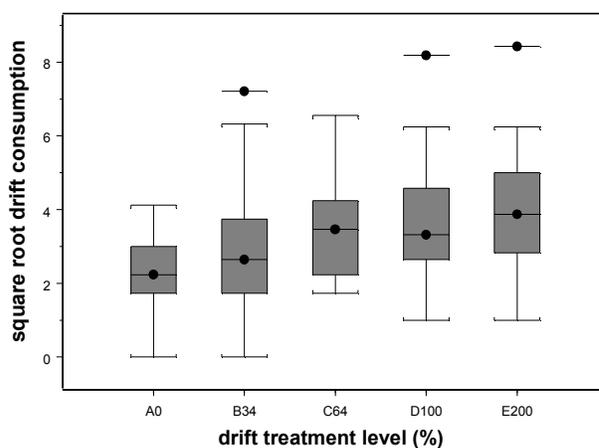


Figure 8.--Moapa dace drift consumption events per 15 min as a function of % natural drift available; whiskers represent 1.5*interquartile range.

Drift availability had no effect on benthic feeding. There was no evidence of a difference in the mean square root of benthic feeding attempts across the five drift treatment levels (p -value = 0.1470 ANOVA F -test). Mean proportional success of benthic feeding also did not differ significantly across the 5 levels (p -value = 0.3453 ANOVA F -test).

Aggressive interactions did not exhibit a discernable trend with drift treatment level. This could not be tested statistically due to a lack of independence between observations of aggressive behavior. Upon viewing the total number of aggressive interactions per level, there does not appear to be a relationship (Appendix 2).

Drift feeding attempts were negatively related to fish length (square root back-transformed; two-sided p -value = 0.0002 from an F -test). Fig. 9 displays a linear fit scatterplot of the number of drift feeding attempts per 15 minutes as a function of fish length in millimeters. For a one millimeter increase in fish length, there was an

estimated decrease of 1.2 (95% confidence interval: 1.4 to 0.8) drift feeding attempts per 15 minutes. There was one outlier, but there is no reason to suspect that this data point is inaccurate. Fish length accounted for 56.1% of the variation in the square root of drift feeding attempts.

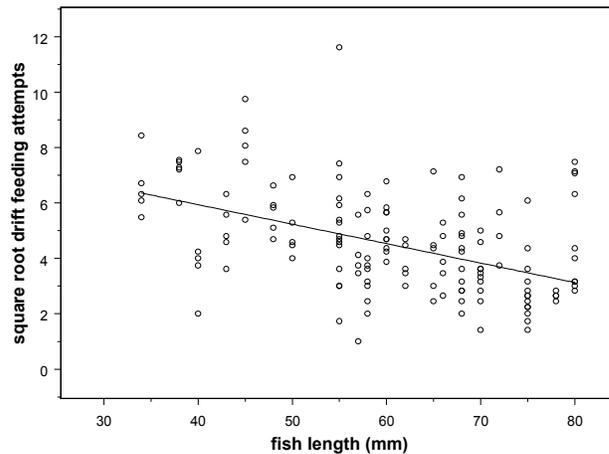


Figure 9.-- Moapa dace drift feeding attempts per 15 min (square root transformed) as a function of their length.

There was no evidence of a relationship between proportional drift feeding success and fish length (two-sided p -value = 0.7784 from an F -test). On average, test subjects drift fed successfully 54% of the time across all treatments. Fish length accounted for 56.1% of the variation in proportional drift feeding success.

Frequency of aggressive interactions was not a function of fish length. This again could not be tested with statistically due to a lack of independence between observations of aggressive behavior.

Discussion

Morphology of a fish species, especially mouth morphology, can provide much insight into a fishes' feeding habits and diet composition. Typically, insectivorous lentic fish with terminal mouths specialize in feeding on drift (Li and Li 2006). In addition to a terminal mouth, these fish also often have a more fusiform body shape, narrower caudal peduncle, and larger caudal fin than their benthic feeding counterparts. These adaptations allow drift feeding fish to have superior swimming capabilities in higher velocities (McLaughlin and Grant 1994). In contrast, fish that specialize on benthic feeding have inferior mouths that open downward (Helfman et al. 2009b). Benthic feeders tend to have broad heads, larger pectoral fins, thicker caudal peduncles, smaller caudal fins, and dorso-ventral flattening (Skulason et al. 1999). These morphological adaptations allow benthic feeders to be more proficient at hunting and avoiding predation in the benthic zone. Fish with subterminal mouths are typically in between these two extremes and tend to be feeding generalists (H. Li & J. Li 2006). Moapa dace have a fusiform body shape typical of a drift feeding fish, but their mouths are subterminal. Their relatively short gut length is typical of a predatory fish, although they do consume some filamentous algae (Scoppettone 1993). Moapa dace have pharyngeal teeth that are strongly hooked but also have a well-developed grinding surface. A gut analysis of 21 individuals indicated an average consumption of 75% macroinvertebrates and 25% plant material (Scoppettone et al. 1992). Moapa dace gut length and pharyngeal teeth structure suggest that this fish is predatory by

nature and requires insects to meet its metabolic needs, but is also capable of omnivory.

Moapa dace did not adaptively shift feeding modes when drift was experimentally reduced. Drift feeding and success were positively correlated with drift level, but benthic feeding was not related to drift abundance. If feeding behavior of Moapa dace was flexible and adaptive to abundance of different food resources, benthic feeding would have increased under reduced-drift conditions. In contrast, Dolly Varden charr, which has head and mouth morphology similar to Moapa dace, readily shifted from drift to benthic foraging when drift was experimentally depleted (Fausch et al. 1997). The study concluded this allows coexistence of Dolly Varden and sympatric white-spotted charr. White-spotted charr is a more obligate midwater and surface feeding fish with a terminal mouth, and exhibited feeding behavior similar to that observed for Moapa dace. When drift was depleted, white-spotted charr did not shift to benthic feeding. Rather, they either fed at a lower rate or emigrated from the study pools (Fausch et al. 1997; Nakano et al. 1999).

Drift feeding attempts and actual consumption events increased with drift level meaning Moapa dace fed more with greater drift availability. Assuming an average maximum of six Moapa dace at a focal site, they could consume 47% of the drift at the lower Pederson representative site. In a few cases as many as 30 Moapa dace have been recorded at a site (author's unpublished data). Considering these numbers, Moapa dace could have a substantial effect on drift abundance and be food limited in some cases. Proportional success in drift feeding increased from 0 to 64% of the

natural drift level and then hit an asymptote. Based on feeding success, it appears that Moapa dace may have reached a maximum food-handling capacity beyond 64% of natural drift and so their efficiency did not increase over that level. However, based on personal observation, that does not seem likely. Moapa dace captured and handled items quickly and never seemed overwhelmed by the density of drift. At low drift levels there were fewer items to choose from so Moapa dace were less discriminate and therefore had higher acceptance rates. At higher drift levels more food was available and less nutritious items were more frequently rejected. In a stream where drift abundance exceeds the food demands of drift feeding fish, handling capacity may not be related to maximum feeding rate until the density of fish causes intraspecific competition (Hansen and Closs 2005; Holbrook and Schmitt 1989).

Number of drift feeding attempts was negatively correlated with fish size. Additionally, proportional success of drift feeding was not related to fish size. This is an unusual outcome because larger individual fish must have greater caloric requirements. Yet, larger individuals fed less frequently and no more successfully than smaller individuals. It could be that larger individuals ingested larger more nutritious food items (Metcalf 1986; Nakano 1995). Some limitations of this experiment were that size and nutrition of actual food items ingested was unknown, and the full spectrum of fish sizes was not represented.

Moapa dace are not aggressive fish. Neither fish size nor drift level had an obvious effect on aggressive behavior. Aggressive interactions were always intraspecific and never directed at springfish. In some cases, a fish species can benefit

from the feeding activity of another species; this activity is known as an interspecific foraging association. Carangid jack (*Caranx latus*), a Brazilian reef fish, employs two methods of feeding. It either searches for prey mid-water, or follows benthic feeding fish and consumes prey that are stirred up from the substrate by the benthic feeder. Carangid jack primarily follows labrid wrasse (*Bodianus rufus*) when exhibiting this behavior. This behavior allows Carangid jack to gain access to more substantial prey items including crustaceans and benthic dwelling fish (Silvano 2001). Moapa dace likely share a similar relationship with springfish. During feeding behavioral observations, this author commonly observed Moapa dace drift feeding directly downstream of benthic feeding springfish. This interspecific feeding association was especially evident during the 0% drift treatment.

Considering the environment they inhabit and their high activity level, energetic costs of Moapa dace must be very high. It is therefore, critical that they feed by the most efficient means possible. Optimal foraging theory states that foragers should accept the most profitable search mode and prey type in terms of energy gained per unit time. An organism would accept less profitable search modes or prey types only when energy gained per unit time falls below a specific threshold (Hughes 1997). Drift feeding is the most profitable feeding method for Moapa dace. If optimal foraging theory applies to Moapa dace, the net energy gained by benthic feeding must ≤ 0 because dace did not shift to benthic feeding. Plausible explanations for this are competition and physiology.

Competition with a more efficient or effective consumer may deter an organism from switching feeding modes. This may be the case with springfish. These fish are more stout and more numerous than Moapa dace. There were approximately eight times the number of springfish as Moapa dace in 1984 in the Muddy River Warm Springs (Scoppettone 1993). This numerical dominance has probably increased due to a decline in the Moapa dace population and an expansion in available habitat for springfish. Springfish spend the majority of their time benthic feeding, dislodging macroinverts from the benthos. If they are more effective competitors at benthic foraging than Moapa dace, it may not be worthwhile for Moapa dace to expend energy searching the benthos. Springfish visually feed more deliberately than Moapa dace (Scoppettone pers. comm.). If Moapa dace cannot compete with springfish, they may benefit by feeding on organisms suspended during springfish benthic feeding activity, similar to the interspecific forage association in reef fish. This interactive feeding was observed in the experimental observation chamber, especially during the 0% drift trial, but was not quantified.

Morphological and physiological characteristics of Moapa dace are related to the physical environment of the Muddy River Warm Springs and are mostly consistent with their feeding. Their extended fusiform body shape is ideal for drift feeding in fast current. Although Moapa dace are capable of omnivory, they are probably less efficient at digesting plant material and detritus than springfish which have a longer relative digestive system (Scoppettone pers. comm.). Benthic feeding fish tend to

consume more plant material, detritus, and sand which is less nutritious and digestible than insects or green algae (Bowen et al. 1995; Grimm 1988).

The subterminal mouth of Moapa dace is inconsistent with the morphology observed in many drift feeding stream fishes. If a fish commonly captured prey drifting below them, a subterminal mouth might be effective. This could happen often during interspecific foraging because invertebrates dislodged by benthic-feeding springfish would initially be drifting near the bottom of the channel. Another possibility is that Moapa dace evolved from a benthic feeding fish. Without the presence of another drift feeding species, selection pressure may not have been great enough to evolve a fully terminal mouth. However, there is scant data on the phylogeny of Moapa dace and co-occurring species (Smith 1981).

Moapa dace have not developed the life-history characteristic to adaptively shift their feeding behavior under reduced-drift conditions due to the energetic costs in an extreme environment and to the presence of benthic-feeding springfish. Life history traits have been linked to extinction risk (Olden et al. 2008). Moapa dace exhibit life history traits associated with elevated extinction risk including specialized feeding, asynchronous reproduction, no parental care, small body size, and limited distribution and dispersal (Scoppettone et al. 1992; Olden et al. 2008). These factors can act in concert with other threats such as habitat loss and competition with invasive species to jeopardize a species (Olden et al. 2008).

Winemiller and Rose (1992) proposed a triangular life history model to explain fishes' adaptive response to environmental variation. The three endpoints are life

history types: 1) opportunistic, characterized by short generation time, high reproductive effort, small body size, low fecundity per spawning event, and low investment per offspring, 2) periodic, characterized by long generation time, moderate reproductive effort, large body size, high fecundity per spawning event, and low investment per offspring, and 3) equilibrium, characterized by longer generation time, low reproductive effort, variable body size, low fecundity per spawning event, and high investment per offspring. In this model, fish with equilibrium life history strategies are associated with stable environmental conditions and predictable resources. In contrast, the opportunistic life history is associated with greater environmental disturbance and lower resource predictability (Winemiller and Rose 1992; Winemiller 2005). Moapa dace fit into the opportunistic life history type in Winemiller and Rose's model but they do not occupy a frequently disturbed environment as predicted for opportunists. The unique environmental conditions of the Muddy River Warm Springs (environmentally extreme but very stable) are not precisely represented in this model.

Desert spring environments, in contrast to higher order reaches of streams in arid region, tend to be extreme and are often stable, yet native fish fauna are typically opportunistic (Constantz 1981; Scoppetone 1992; Winemiller and Rose 1992). In this apparent departure from the Winemiller and Rose (1992) model, we propose that environmental stresses override disturbance frequency. Physiological stresses influence life history traits to allow species to persist in isolated and environmentally limiting habitats. Small desert fishes have persisted in relict habitat through high

demographic resilience associated with opportunistic life histories. Forty percent of endangered species are classified as opportunistic even though they make up only 30% of continental fish fauna. Therefore opportunists are at a disproportionately increased risk to extinction (Winemiller 2005).

Habitats of desert spring-dwelling fishes are so small, isolated, and fragile, that they are at great risk of decimation. Isolated desert fish populations are essentially “island” populations which exhibit higher extinction rates than “mainland” populations due to dispersal limitations (Diamond 1975). Introduction of fish that are equally fecund and tolerant to adverse environmental conditions poses an additional threat to native desert fishes. Invasive species can compete with and consume native fish at various life stages (Scoppettone 1993). The observed obligate feeding behavior and unique life history traits in Moapa dace demonstrate the importance of habitat preservation and exclusion of invasive species as essential management practices to maintain endangered and isolated desert fish populations.

Conclusion

Moapa dace are highly active thermophilic minnows that exist in a demanding environment through obligate drift feeding. Despite similarities with other fish species capable of adaptive shifts in feeding modes, Moapa dace did not shift to benthic feeding when drift was reduced. Moapa dace feed more at higher drift levels. Although their efficiency does not seem to improve at the highest drift levels, they may be able to feed more selectively on the highest quality items when drift levels are

relatively high. Based on observations of aggressive behavior, Moapa dace compete with one another for food resources. In contrast, Moapa dace probably share an interspecific forage association with springfish that is beneficial to Moapa dace. By consuming and assimilating more calories through this behavior, Moapa dace survival and fecundity may be greater (Mann 1974; Mann and Mills 1985). Maintaining in-stream flows and restoring habitat to promote a productive drifting macroinvertebrate community would likely aid in Moapa dace recovery.

Acknowledgements

Thanks to Dr. Stan Gregory (Department of Fisheries and Wildlife, Oregon State University) for guidance and moral support. Thanks to Dr. Matt Mesa (USGS, Western Fisheries Research Center, Columbia River Research Lab) for supporting this work through a research assistantship. Thanks to Becky Flitcroft for statistical advice. Thanks to Chris Dixon and many volunteers for assisting in some extremely hot field conditions.

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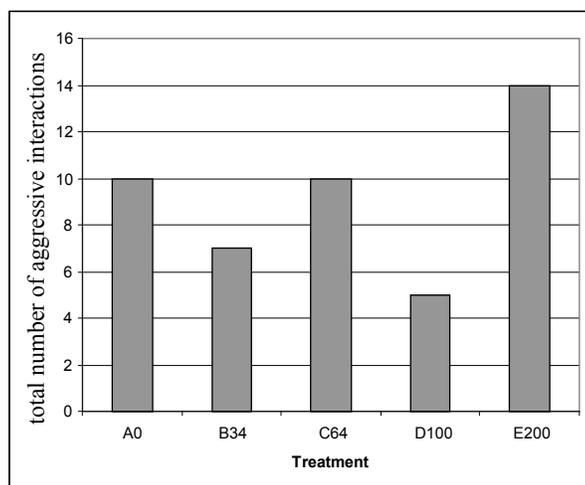
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Appendices

A1. Square root back transformed estimated means and 95% confidence intervals of Moapa dace drift feeding attempts per 15 minutes.

Treatment (%)	lower	est.	upper
0	8.99	13.17	18.15
34	7.80	16.06	27.28
64	10.90	20.40	32.84
100	12.04	21.94	34.79
200	17.55	29.20	43.80

A2. Total number of aggressive interactions per treatment



CHAPTER 5: SYNTHESIS CONCLUSION

By examining the food web structure across a range of environmental conditions that are currently existent in the Muddy River Warm Springs, we can make informed predictions of how the aquatic community structure might change if environmental conditions change. If the amount of available warm water habitat decreases in the future, communities that now exist in cooler reaches may come to dominate more of the system. Since cooler reaches are currently dominated by invasive species, this would clearly be undesirable.

Using a hierarchical research strategy, we began with a broad view of food web dynamics by using stable isotopes to gain a basic understanding of nutrient cycling and trophic dynamics in this system. This gave us a sense of what Moapa dace are consuming and where their nutrient sources originated. In the third chapter we narrowed our focus to food supply for Moapa dace and its relationship with current environmental conditions. This allowed us to explore different components of the food base and whether macroinvertebrates consumed by Moapa dace were commensurate with what was available in the drift. In the fourth chapter, we zeroed in on Moapa dace feeding to determine if any behavioral limitations exist.

Contrary to our predictions, we found that allochthonous inputs are the primary nutrient source in this system. This suggests that food web productivity in the Muddy River Warm Springs is dependent on labile forms of riparian vegetation. Habitat restoration activities should focus some attention on these types of native vegetation. Different macroinvertebrate orders did not exhibit distinctive isotopic signatures so we

could not determine specific food preferences of Moapa dace from these results. We also found that $\delta^{13}\text{C}$ signatures of primary producers increase substantially in a downstream direction. This phenomenon appears to be common in groundwater-fed spring systems, but has received very little attention in the literature (Doctor et al. 2008). Investigators conducting isotope analyses in spring systems should consider this pattern when interpreting results.

We found greater drift abundance in lower reaches of potential Moapa dace habitat. Currently, this habitat is inaccessible to Moapa dace because managers have erected fish barriers to keep non-native blue tilapia from invading remaining dace refugia. This research supports the current management plan of reclaiming stream reaches with rotenone treatment and removing fish barriers in a downstream direction. When Moapa dace can freely access lower reaches, like the main stem of the Muddy River, they will likely grow larger and more abundant as a result of access to greater food resources. Based on historic accounts of large individuals in lower reaches and spawning observed only at springheads, Moapa dace may naturally have a fluvial life history pattern where they spawn and rear in the smaller headwaters and live as adults in the lower, larger reaches (Scoppettone et al. 1992).

Drift availability could change as a result of altered hydrologic and thermal conditions. We wanted to know if Moapa dace would be able to adapt to changes in drift availability by shifting feeding modes like Dolly Varden charr (Fausch et al. 1997). Moapa dace did not shift feeding modes when drift was reduced. This important finding suggests that Moapa dace would not adapt well to reductions in

drift. Considering physiological challenges posed by the thermal spring environment and the current status of Moapa dace, a reduction in drift as a result of declining spring discharges could be catastrophic to this population. Desert fishes that are endemic, restricted to a small area, occupants of one drainage basin, and found in warm water streams are at the greatest risk of extinction (Moyle and Williams 1990). Moapa dace have all of these characteristics.

What chance does this tiny desert minnow have in the face of habitat loss, the booming development of the Las Vegas area, and climate change? It depends on our perspective. We have a very good idea of how to recover this species, but it hinges on public will. How do you explain the value of biodiversity to the general public? The most convincing answers are those that reference our own well being. If specific human activities are causing extinctions, those activities have real implications on our own health and survival into the future.

“Whether we and our politicians know it or not, Nature is party to all our deals and decisions, and she has more votes, a longer memory, and a sterner sense of justice than we do.” Wendell Berry

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