

Predators Lack Complementarity in a Degraded Stream

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Anthropogenic disturbance has led to the loss of biodiversity, altering ecosystem processes and decreasing stability. Top predators have been disproportionately affected by this degradation. Functional complementarity via niche overlap is one mechanism by which ecosystem processes may be maintained in the absence of a top predator. Aquatic ecosystems have shown a decline in top predators such as salmonids, but few studies have addressed the functional complementarity of alternative predators. In beaver ponds in the western U.S., Western Tiger Salamanders (*Ambystoma mavortium*) often become the top aquatic predator in the absence of fish, yet no previous studies have explored their trophic ecology. We evaluated this knowledge gap and used criteria including population size structure, diet, and stable isotope analysis to investigate the functional complementarity of a degradation tolerant species, the Arizona Tiger Salamander (*A. m. nebulosum*), compared to the native but extirpated salmonid top predator, Colorado River Cutthroat Trout (*Oncorhynchus clarkii pleuriticus*). Field data for tiger salamanders and published accounts of various salmonid species suggested that, although both species are characterized by size-structured populations with ontogenetic shifts in a generalist diet, the trophic position of *A. m. nebulosum* is lower than reported values for large salmonids. This lower trophic positioning suggests that salamanders are likely to be functionally complementary with only the smallest size classes of salmonids. These results support previous work suggesting that functional complementarity exists under a narrow range of environmental conditions, which may limit the degree to which degradation-tolerant species can maintain communities.

EARTH has been drastically altered by human activity, though the scope and consequences of these changes are not fully understood. Anthropogenic disturbance has been shown to negatively affect ecosystem biodiversity (montane forests: Veblen and Lorenz, 1986; coastal shores: Benedetti-Cecchi, 2001; deserts: Lovich and Bainbridge, 1999). This loss of biodiversity can lead to decreased community stability and ecosystem functionality as complex interactions within communities are altered (Tilman, 1999). There is thus a need to better understand the ecological consequences of anthropogenic disturbance.

Biodiversity loss is a consequence of disturbance that can have wide-reaching ecosystem effects. Individuals at the highest trophic level appear to be disproportionately affected by modern threats such as climate change and other anthropogenic impacts (Duffy, 2003; Estes et al., 2011; Ripple et al., 2014). Specific threats to top predators include overexploitation by humans (Estes et al., 2011), habitat loss and fragmentation (Duffy, 2003; McManus et al., 2015), heavy metal pollution (Suedel et al., 1994), and invasion by non-native organisms (Eby et al., 2006; Tronstad et al., 2010). Although much focus has been placed on conservation efforts such as protecting remaining populations of at-risk predators and restoring native top-predators (Fritts et al., 1997; Balme et al., 2010; Vera et al., 2013), it is also important to understand how community interactions and ecosystem processes differ in these altered systems. For example, loss of a top predator can modify food-web structure and affect ecosystem function (Morin and Lawler, 1995; Post, 2002; Power and Dietrich, 2002; Estes et al., 2011; Terborgh, 2015), yet we have little understanding of how remaining or newly colonizing predators might impact ecological interactions and processes. Investigating the consequences of biodiversity loss in such degraded systems is important for the management and restoration of impacted ecosystems.

Central to the study of altered food webs is the concept of functional redundancy (Root, 1967); particularly, whether

community members with comparable niches persist after disturbance, maintaining ecosystem function and stabilizing communities (Naeem, 1998; Hubbell, 2005, 2006). As complete niche redundancy has yet to be observed in nature, the term functional complementarity, which is the sharing of similar niches by multiple species so that ecosystem processes are maintained if one species is lost, is more appropriate (Kurzava and Morin, 1998; Resetarits and Chalcraft, 2007; Thibault et al., 2010). For example, after predator extirpation the presence of one or more remaining species with similar foraging preferences could help maintain communities and ecosystem processes (Walker, 1992; Naeem, 1998). This maintenance of communities by complementary predators may be particularly important in systems with strong top-down control, since the loss of a top predator in systems with trophic cascades can result in sweeping changes in community dynamics that radiate through a food web (Paine, 1966; Estes and Palmisano, 1974; Carpenter et al., 1985; Power, 1992).

Many aquatic ecosystems have experienced rapid declines of top-predators (Pauly et al., 1998; Baum et al., 2003; Myers and Worm, 2003; Rush et al., 2012), resulting in strong trophic cascades in some systems (Scheffer et al., 2005; Myers et al., 2007; Heithaus et al., 2008). In freshwater systems, loss of salmonid top predators due to disturbance is particularly severe (Kruse et al., 2000; D'Angelo and Muhlfeld, 2013). A major conservation effort has been the restoration of native salmonid populations to anthropogenically degraded streams, though how these stream communities function in the absence of fish predators is not well understood (Shepard et al., 2005). This is particularly important as salmonids can induce trophic cascades, so their extirpation from a system could have wide-reaching community effects (Power, 1992; Konishi et al., 2001; Simon and Townsend, 2003).

Amphibians are a possible surrogate for predatory salmonids in disturbed ecosystems, although the relationship between fish and amphibians is complex. In some systems

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where members of both groups have coevolved, amphibians and salmonids coexist (Resetaarits, 1995; Sepulveda et al., 2012). In many systems, however, salmonids are able to prey on vulnerable amphibian life stages, preventing coexistence and decimating native amphibian populations (Gillespie, 2001; Bradford et al., 2003; Lowe et al., 2004; Vredenburg, 2004). Although negative effects of salmonids on amphibians have been well studied, there has been little research on how amphibians respond to loss of salmonids from a system. Of particular interest is whether amphibians can fill the trophic role of a piscivorous top predator, preserving trophic structure. Most amphibians have terrestrial life stages as part of their complex life cycle, allowing them to disperse by land from off-site refugia and readily colonize disturbed habitats that may remain inaccessible to fish due to variable hydrology, water temperature, or colonization barriers such as dams (Pess et al., 2012). Little is known of the trophic role of amphibian top predators in traditionally fish-dominated systems, but continued loss of native-fish populations as a consequence of disturbance suggests that focused research on these questions is warranted. Such research is particularly timely as disturbed systems are likely to persist and become more common via climate change-induced drought (Dai, 2013).

In the western United States, the Arizona Tiger Salamander (*Ambystoma mavortium nebulosum*) can breed in streams in the absence of native salmonids (K. Boeckman, pers. obs.). Although they act as top predators in lentic ponds (Dodson and Dodson, 1971; Collins and Holomuzki, 1984; Wissinger et al., 1999), little is known about the trophic ecology of larval salamanders in lotic beaver ponds. Due to similar feeding morphology and diet overlap, *Ambystoma* have been likened to “a fish in amphibian’s garments” (Zaret, 1980). Gray Tiger Salamanders (*Ambystoma mavortium diabolii*) in prairie pothole systems have been found to have diets similar to planktivorous fish (Benoy, 2008) and the trophic position of Axolotls (*Ambystoma mexicanum*) in Lake Xochimilco was found to be higher than non-native Common Carp (*Cyprinus carpio*) and Tilapia (*Oreochromis niloticus*; Zambrano et al., 2010) supporting Zaret’s hypothesis for planktivorous, but not piscivorous, fish. Functional complementarity of tiger salamanders to salmonids thus has the potential for substantial community consequences.

In an effort to better understand the role of amphibians as top predators in disturbed systems, dietary, community, and stable isotope data were used to characterize the trophic ecology of *A. m. nebulosum* in beaver ponds of a degraded stream formerly inhabited by Colorado River Cutthroat Trout (*Oncorhynchus clarkii pleuriticus*). These data were compared with data from the literature to evaluate the trophic complementarity of *A. m. nebulosum* and salmonids. We predicted that the trophic ecology of the larger, older age classes of salamander larvae would more closely resemble that of salmonids in beaver ponds, as measured through diet composition, electivity, and trophic position (Browne and Rasmussen, 2011; Whiting et al., 2014). Additionally, we used data from this study as well as the literature to evaluate size structure and life history of both amphibians and fish to examine actual and potential complementarity of *A. m. nebulosum* and salmonids in lotic beaver pond systems.

MATERIALS AND METHODS

Study site.—Kimball Creek is a third order stream that lies ~50 kilometers northeast of Grand Junction, Colorado. The

stream has been degraded by years of overgrazing, beaver removal, and irrigation for agricultural use, resulting in a loss of riparian area and deeply incised channel morphology (R. Lee, pers. comm.). The degradation in Kimball Creek occurs across a gradient, with the most incision and riparian loss occurring near Down Valley reaches. Upper Valley areas have been less degraded by grazing and irrigation; the Upper Valley has less bank erosion and more intact riparian zones than Down Valley or Mid-Valley reaches. Natural recolonization of beaver populations has led to pond construction along the length of Kimball Creek. Historical populations of Colorado River Cutthroat Trout have been extirpated from the stream, and the current aquatic top predator is *A. m. nebulosum* (R. Lee, pers. comm.; K. Boeckman, pers. obs.).

Study organism.—*Ambystoma m. nebulosum* is native to the western United States, with a range that extends from western Colorado and Utah to central Arizona and New Mexico (Behler and King, 1979), and is a common predator in fishless Colorado lentic systems (Dodson and Dodson, 1971; Hammerson, 1999). Terrestrial adults (metamorphs) of this species breed in Kimball Creek beaver ponds. Aquatic larvae feed and grow in the ponds before metamorphosing into terrestrial adults. The length of time larvae spend in ponds varies widely, with some young-of-year (hatchling) larvae metamorphosing at the end of their first summer, whereas others overwinter in ponds, metamorphosing during their second summer (2nd year larvae; K. Boeckman, pers. obs.).

Salamander sampling.—Populations of *A. m. nebulosum* were sampled with a seine in all accessible Kimball Creek beaver ponds from early June to early August of 2012 and 2013. Salamanders were collected and kept in minnow buckets until being processed on site. Individuals were weighed (g), and measured for snout to vent (SVL) and total length (mm). Gape width (mm), gill health, and condition were also recorded for all individuals. Year-to-year differences in beaver pond hydrology and salamander population size structure necessitated pooling within size classes across years and sites for diet comparisons. The Down Valley beaver pond only held water in the 2012 field season and supported the only population of 2nd year larvae sampled during that year. The Mid-Valley and Upper Valley pond complexes (each of which contained 3 to 4 ponds) held water for both seasons, but only contained 2nd year larvae during the 2013 season.

To evaluate salamander diet composition, stomach samples of all available size classes were collected via gastric lavage (Joly, 1987) from 3–5 individuals per pond during the 2012 field season and ten individuals per pond during 2013. To reduce the effects of seasonal variation, salamander diet and pond community data were collected from a single pond in each complex in late July of each year. All diet samples were stored in 70% ethanol for examination in the laboratory. Head width and body length (when possible) were recorded for each prey item. Head width-mass regressions for each taxon were used to calculate ash-free dry mass (AFDM; Benke et al., 1999). Although length-mass regressions are more readily available and widely used in the literature, diet samples infrequently contained intact prey. Infrequently encountered prey (<2.0% of total biomass or abundance) were lumped together as “Miscellaneous” and included terrestrial prey, Notonectidae, Bivalvia, Oligochaeta, and Hirudinea. Diet composition for 2nd year larvae was compared across sites using MANOVA for both abundance and

biomass (AFDM). Transformations of data were performed when necessary to obtain normality. Tukey *post hoc* tests were used to detect differences between sites for individual prey species.

Benthic invertebrate community sampling.—During the 2013 season, four sediment core samples were taken from each pond to quantify benthic community composition simultaneous with salamander diet samples (Hauer and Lamberti, 2007). A benthic corer (sampling area = 314 cm²) was driven into the substrate, and all materials and water were removed to a maximum depth of 10 cm or as far as the substrate allowed. The sample was placed in a graduated bucket and cobble were scrubbed to remove any organic matter or invertebrates. The sample was stirred and elutriated into a 250 µm mesh sieve until all invertebrates and organic materials were removed from heavy inorganic materials. Contents of the sieve were rinsed into a plastic bag, labeled, and preserved in an 8% formalin solution. In the laboratory, all invertebrates from benthic core samples were identified to order or family, counted, and measured for AFDM. Benthic community composition was compared between the two ponds using MANOVA.

Diet electivity.—Larval feeding electivity for 2nd year larvae in 2013 was calculated using Vanderploeg and Scavia's (1979) Relativized Electivity, E_i^* . This index is appropriate for comparisons of electivity across sites as well as data with rare prey types (Lechowicz, 1982). Hatchlings were excluded from this analysis because of size limitations during gastric lavage sampling. The index is calculated as:

$$E_i^* = [W_i - (1/n)]/[W_i + (1/n)] \quad (\text{Eq. 1})$$

$$W_i = [r_i/p_i]/[\sum_i(r_i/p_i)] \quad (\text{Eq. 2})$$

where r_i is the relative abundance of each prey item (i) in the diet sample, p_i is the relative abundance of each prey item in the environment, and n is the number of prey types in the sample. The index ranges from -1 to 1 with random feeding centered around zero, values near -1 indicating avoidance of a food item, and values near 1 indicating preferential feeding on a prey item. One-sample Student's t tests were used to determine whether electivity differed significantly from zero, and non-parametric Wilcoxon rank-sum tests were used to evaluate differences in electivity between sites.

Stable isotope analysis.—During 2013, two sites (Mid-Valley and Upper Valley; Down Valley was excluded because it held no water in 2013) were intensively sampled for stable isotope analyses. Samples were collected from dominant primary producers (filamentous algae, in most cases), detritus, invertebrates (Corixidae, Ephemeroptera, Dytiscidae, Diptera, Odonata, and Gastropoda), and larvae of *A. m. nebulosum*. Toe and tail clips were taken from the salamanders for analysis, while all invertebrates were collected whole. Toe and tail clips have been shown to be suitable non-lethal samples for stable isotope analysis in amphibians (Finlay and Vredenburg, 2007; Milanovich and Maerz, 2012). At the time of sampling, no 2nd year larvae remained at the Upper Valley site. Samples were stored in Whirl-Paks or scintillation vials, and invertebrates were starved for 24 hours to allow the digestive tract to clear before freezing (Fry, 2006). Samples were dried and ground to a fine powder using a ceramic mortar and pestle. Small organisms of the

same taxonomic classification were combined to provide an adequate sample mass. Ground samples were weighed, and between 0.5 and 3.00 milligrams of each sample was placed in 8x5 mm Elemental Microanalysis Ltd. tin capsules. The samples were analyzed using a Finnigan Delta Plus XP mass spectrometer at Murray State University's Hancock Biological Station.

Means and 95% confidence intervals for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were calculated for each taxon. Trophic positions were estimated with the formula:

$$\text{TP}_{\text{consumer}} = [(\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/3.4] + 2 \quad (\text{Eq. 3})$$

where $\delta^{15}\text{N}_{\text{consumer}}$ is the $\delta^{15}\text{N}$ value of the taxon in question, $\delta^{15}\text{N}_{\text{baseline}}$ is the $\delta^{15}\text{N}$ value for the baseline macroinvertebrate sample, 2 is the estimated trophic position of the baseline organism (an herbivore), and 3.4 is the estimated shift between trophic levels (Minagawa and Wada, 1984; Post, 2002). The mean $\delta^{15}\text{N}$ value for Ephemeroptera was used as the baseline $\delta^{15}\text{N}$ because it was ubiquitous across diet samples and common in the environment.

All statistical analyses were conducted using R version 3.0.3 (R Core Team, 2013).

RESULTS

Salamander diet.—Larval diet composition varied between size classes within the Down Valley site during the 2012 field season (Fig. 1; MANOVA: biomass: $F_{7,26} = 7.1$, $P < 0.001$; abundance: $F_{7,26} = 10.4$, $P < 0.001$). Hatchling diet biomass was dominated by Ephemeroptera (52.2%), Corixidae (16.0%), and dipterans (10.0%). The most abundant hatchling prey item was zooplankton (33.3%), but the small size of this prey type resulted in zooplankton comprising only 5.0% of total hatchling diet biomass. Ephemeroptera also contributed the largest proportion to 2nd year diet by abundance (43.3%) with Corixidae contributing 41.4%. Second year larval diet biomass was dominated by Corixidae (52.3%) and Ephemeroptera (39.6%) with all other diet groups composing less than 5% individually. Abundance and biomass for Corixidae and zooplankton was significantly different between the two larval size classes (Tukey contrasts; both $P < 0.001$).

Diet composition of 2nd year larvae showed significant variation across sites, as indicated by overall MANOVA results for abundance ($F_{12,100} = 12.0$, $P < 0.001$) and biomass ($F_{12,100} = 14.7$, $P < 0.001$; Fig. 2A, B). Across the three sites, differences in abundance were attributed to Ephemeroptera ($P < 0.001$), Dytiscidae ($P < 0.001$), Corixidae ($P < 0.001$), Diptera ($P < 0.001$), and Odonata ($P < 0.01$). Biomass also differed among sites for Dytiscidae ($P < 0.001$), Corixidae ($P < 0.001$), Diptera ($P < 0.001$), Odonata ($P < 0.01$), and miscellaneous prey ($P < 0.001$). *Post hoc* analysis indicated that differences in abundance were attributed to higher Corixidae proportions in Down Valley, higher Ephemeroptera proportions in Mid-Valley, and lower Odonata and higher Dytiscidae values in Upper Valley diets. Differences in biomass were attributed to lower Diptera and higher miscellaneous values in Down Valley and higher Dytiscidae and lower Odonata values in Upper Valley relative to the other sites (all Tukey contrasts $P < 0.01$). Tukey contrasts also indicated that dipteran abundance was significantly lower in Down Valley relative to the other two sites ($P < 0.01$), and dipteran biomass in salamander diets decreased from Upper Valley to Down Valley ($P < 0.05$).

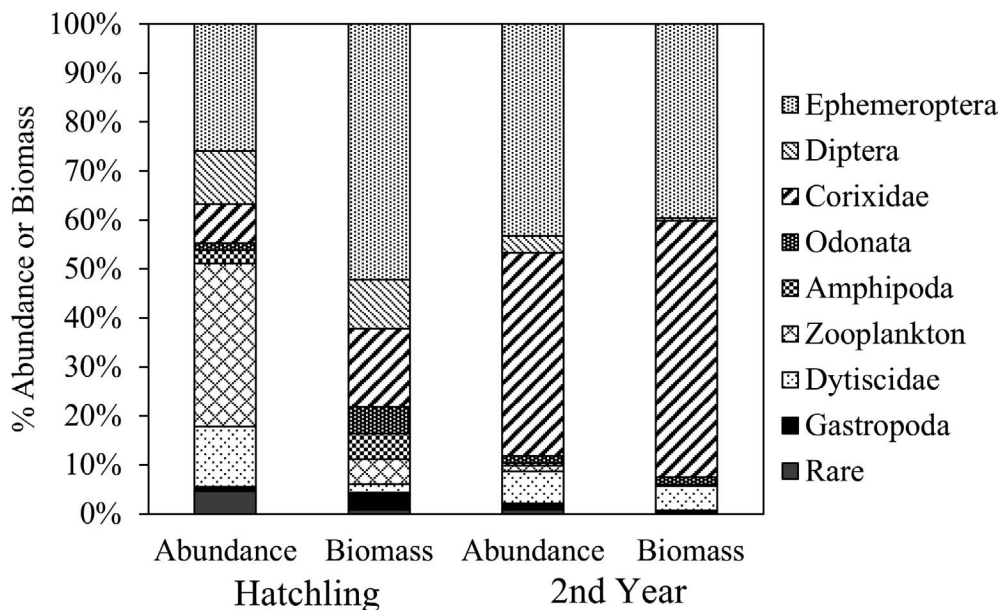


Fig. 1. Comparison of 2nd year and hatchling Arizona Tiger Salamander (*A. m. nebulosum*) dietary abundance and biomass (AFDM) during the 2012 field season across ponds in Kimball Creek in western Colorado.

Benthic invertebrate community and diet electivity.—Benthic invertebrate communities did not differ between Upper Valley and Mid-Valley for abundance (MANOVA: $F_{1,6} = 7.26$, $P = 0.28$) or biomass (MANOVA: $F_{1,6} = 43.29$, $P = 0.12$). However, electivity (E^*) of 2nd year larvae differed between Upper Valley and Mid-Valley. Larvae in the Mid-Valley site preferentially fed on Ephemeroptera and Dytiscidae, whereas larvae from Upper Valley preferred only Dytiscidae. Larvae from both ponds avoided Amphipoda, Hirudinea, Notonectidae, and Gastropoda. Additionally, Mid-Valley larvae avoided Odonata and Diptera, and Upper Valley larvae avoided Ephemeroptera. Significant differences in electivity values for the two ponds existed for Ephemeroptera ($W = 2$; $P < 0.001$) and Amphipoda ($W = 5$; $P < 0.001$). Overall electivity for Upper Valley and Mid-Valley was very similar, with the majority of prey items either consumed at random or avoided. The most divergent taxon between sites was Ephemeroptera, which was preferred by Mid-Valley larvae but avoided by Upper Valley larvae.

Stable isotope analysis.—Stable isotope analysis revealed that $\delta^{15}\text{N}$ values were enriched in all Upper Valley samples relative to their Mid-Valley counterparts (Fig. 3). In both sites, larval salamanders were the most $\delta^{15}\text{N}$ -enriched consumers, though only Mid-Valley contained 2nd year larvae during stable isotope sample collection. Some uncharacteristically low (Mid-Valley algae) and high (Upper Valley algae) $\delta^{15}\text{N}$ values suggest potential error in sampling or processing.

Although Upper Valley samples contained higher $\delta^{15}\text{N}$ values, the trophic position for hatchling larvae in Upper Valley (2.80 ± 0.03) and Mid-Valley (2.90 ± 0.05) was similar (Table 1). The trophic position for 2nd year larvae in Mid-Valley (3.66 ± 0.05) indicated that these larger larvae were feeding at a trophic level approximately 0.67 levels higher than hatchlings.

DISCUSSION

As anthropogenic disturbance continues to alter ecosystems, it is increasingly important to understand how disturbed ecosystems function. The loss of top predators in aquatic ecosystems has the potential to result in cascading changes

across food webs. Research on the complementary role of amphibians and native fish predators is important for the management of degraded systems. To investigate the trophic role of amphibians in the absence of native fish, we evaluated diet and trophic position of *A. m. nebulosum* to better understand the trophic ecology of this degradation-tolerant species, and to evaluate complementarity with salmonids. Our results suggest that salamanders are not broadly complementary to salmonids.

Salamander diets varied across ontogeny and site. Similar to results found for lentic-pond communities, diet composition differed between hatchling and 2nd year larvae in beaver ponds (Dodson and Dodson, 1971; Collins and Holomuzki, 1984; Holomuzki and Collins, 1987; Zerba and Collins, 1992). Ephemeropterans were a major prey for both sizes of larvae, in terms of both abundance and biomass. Differences in diet were the result of a greater proportion of larger prey (Corixidae) in 2nd year diets and zooplankton in hatchling diets, supporting previously reported gape-limited feeding by *A. m. nebulosum* (Zaret, 1980; Wissinger et al., 1999). Electivity values for 2nd year larvae varied between the Upper Valley and Mid-Valley sites, with little preference for most prey taxa, suggesting a generalist feeding strategy (Wissinger et al., 1999). Differences in electivity between Mid-Valley and Upper Valley may be attributed in part to differences in vegetation in the two ponds. While Mid-Valley had macrophytes that may have provided refuge for invertebrates throughout the water column (Rantala et al., 2004; Denno et al., 2005), Upper Valley was dominated by mats of filamentous algae that floated at the surface of the water.

Like the salamander larvae in this study, salmonid diets have also been shown to shift with ontogeny, with small size classes depending more on invertebrate prey and large trout preying on fish (Table 1; Nowak et al., 2004; Ayllon et al., 2010). Diet data for trout in beaver ponds is limited, but a study of Brook and Cutthroat trout in Idaho streams found that both species (95–281mm in snout-fork length) consumed over 80% dipteran larvae by abundance when in beaver ponds and less than one percent Ephemeroptera (Hilderbrand and Kershner, 2004). An earlier study of Brook Trout in a Wyoming beaver pond found that Ephemeroptera was the most common prey item across fish size classes, but

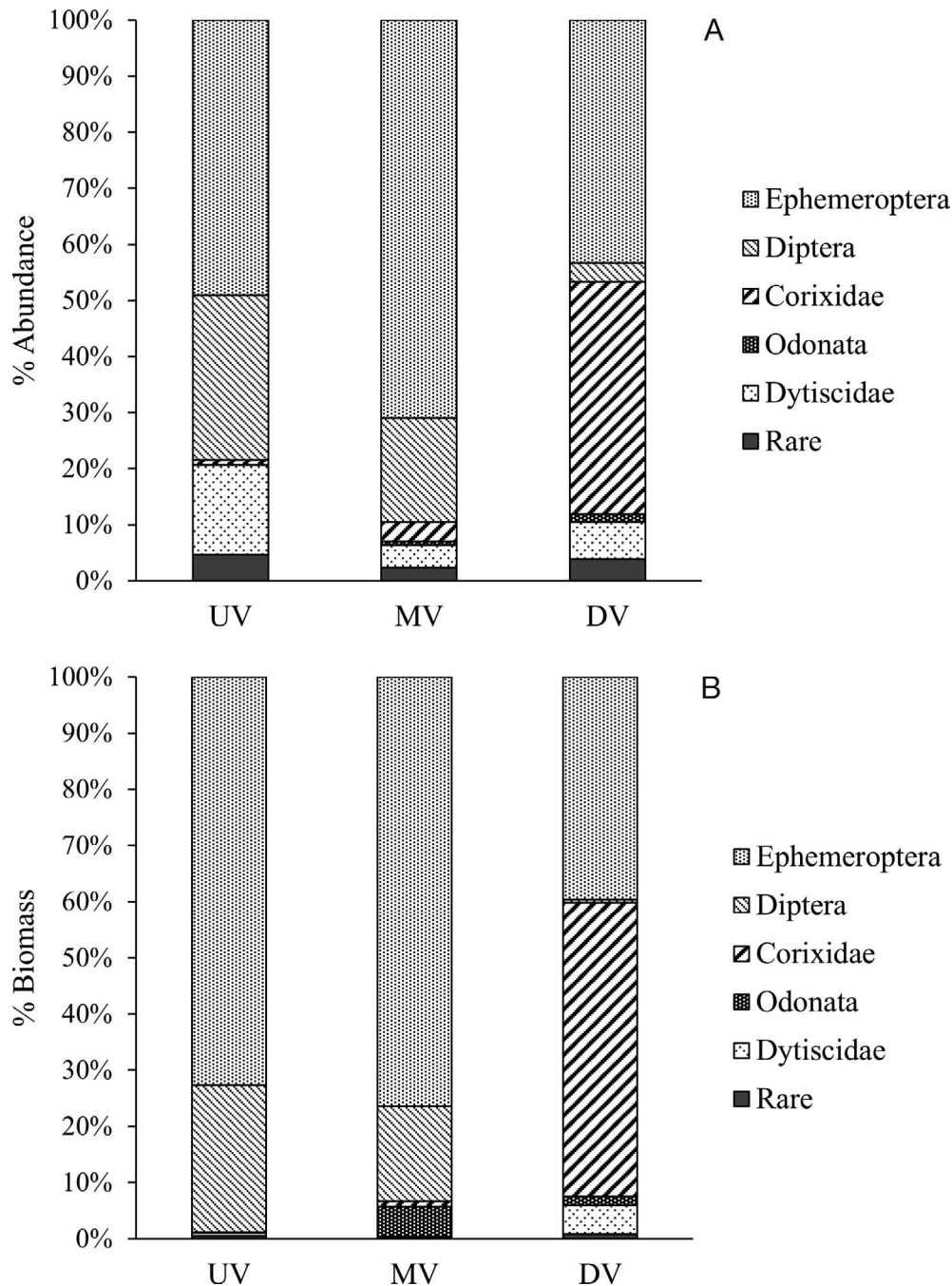


Fig. 2. Diet composition of 2nd year larvae across three Kimball Creek sites (UV = Upper Valley, MV = Mid-Valley, DV = Down Valley) by percent of total abundance (A) and biomass (B).

that larger fish consumed more adult Coleoptera and Diptera (Allen and Claussen, 1960). In both studies, diet electivity was low, suggesting similar generalist feeding by both salamander larvae and salmonids in beaver ponds.

Stable isotope data also revealed differences between sites and salamander size classes. Stable isotope data provide a more accurate reflection of diet and trophic position over time. The cause of large $\delta^{15}\text{N}$ differences between larvae from Upper Valley and Mid-Valley sites is unclear, but may be attributed to differences associated with the position of these pond complexes in the valley, including the time that cattle typically spend near or above these reaches (Harrington et al., 1998; Rosario et al., 2002) or differences in pond morphology and water retention within each site. In both complexes, larval salamanders were the top predators, having the highest $\delta^{15}\text{N}$ enrichment in the food web. Second year larvae had a $\sim 3\text{‰}$ enrichment over hatchling salamanders, which had

$\delta^{15}\text{N}$ values similar to Odonata and Notonectidae, both invertebrate predators. In the absence of 2nd year larvae (Upper Valley), hatchling larvae showed trophic separation from these invertebrate predators, although the trophic position of hatchling larvae remained the same, indicating invertebrate predators fed at lower trophic levels in Upper Valley than in Mid-Valley (Fig. 3), perhaps because of the lack of refugia described above. Some uncharacteristically low (MV algae) and high (UV algae) $\delta^{15}\text{N}$ values suggest potential error in sampling or processing. As primary producers were not included in the calculation of trophic position, these values did not affect the calculations used for comparisons across studies.

A useful tool in interpreting stable isotope results is the calculation of trophic position, which gives a trophic value for consumers using baseline data unique to each community. The trophic position of hatchling salamanders did not

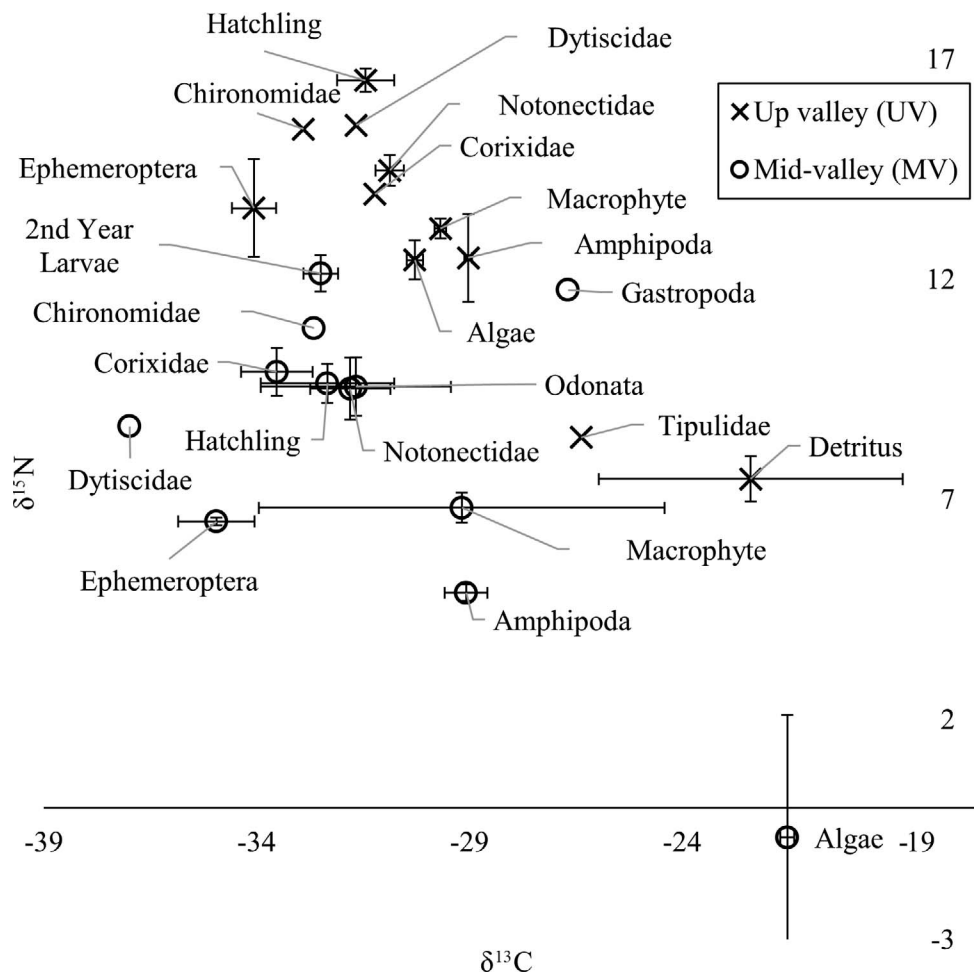


Fig. 3. Stable isotope results for Upper Valley (UV, X) and Mid-Valley (MV, circles). Bars represent 95% confidence interval.

differ between Upper Valley and Mid-Valley, suggesting that the role of hatchling larvae as predators was the same at each site. The trophic position of 2nd year larvae was higher than hatchlings by 0.67 trophic levels. Thus, 2nd year larvae are top predators in this size-structured system, feeding on a larger proportion of aquatic predators, enriching their $\delta^{15}\text{N}$ values. Trophic positions of salmonids in beaver ponds was not available for comparison, but several studies have calculated values for trout in other systems (Table 1). The trophic position of large salmonids was frequently calculated at the fourth trophic level or higher, whereas smaller size classes fell closer to the range observed in *A. m. nebulosum* in Kimball Creek. Higher trophic values of larvae of *A. m. nebulosum* would only have the potential to approach trophic position values reported for larger trout if there were a high degree of cannibalism in the population, which is common in this species, though not observed in this study (Collins and Holomuzki, 1984; Lannoo and Bachmann, 1984; Whiteman et al., 2003; Wissinger et al., 2010).

In addition to diet and stable isotope data, behavioral and life history traits have the potential to affect the functional complementarity of salamanders and salmonids. Across Kimball Creek beaver ponds, a wide range of larval salamander size structures and densities have been found, ranging from ponds with low densities of 2nd year larvae and high densities of hatchlings to ponds that support high densities of 2nd year larvae and extremely low densities of hatchling larvae (K. Boeckman, pers. obs.). The size- and age-specific differences in diet detailed above have potential community consequences via trophic interactions and

suggest that, by mass, hatchling and 2nd year larvae have the potential to differentially affect pond ecosystems. Salmonid populations in Rocky Mountain beaver ponds have also been found to vary in size structure. For example, in some systems, large, deep ponds tended to contain large fish at low densities, while smaller, shallower ponds were composed of high densities of small fish (Rabe, 1970; see also Keast and Fox, 1990; Johnson et al., 1992). With potential to alter trophic dynamics, size structure of predator populations is an important factor regulating the complementarity of salamanders and salmonids that warrants further research.

Although outside the scope of this study, how individual prey respond to salmonid and salamander presence in a system is an important component of functional complementarity. This is particularly true since non-consumptive effects have been shown to be of great importance in many trophic cascades (Schmitz et al., 1997; Preisser et al., 2005). For example, research suggests that responses by Ephemeroptera to the two predators could be quite different. In *Callibaetis*, a common pond mayfly genus, ponds with trout have been found to be population sinks (Caudill and Peckarsky, 2003; Caudill, 2005), perhaps because they show no avoidance of salmonids when selecting ponds for oviposition (Caudill, 2003). *Callibaetis* are thought to have evolved in temporary, fishless environments, making their antipredator behaviors such as high activity rates better suited for predators typically found in these temporary ponds, such as *A. m. nebulosum* and adult Dytiscidae (Caudill and Peckarsky, 2003). This difference in antipredator responses to fish and salamanders could decrease

Table 1. Reported length, primary prey type, and trophic positions (TP) of salamanders and salmonids.

Habitat	Species	Size (mm)	Primary prey items	TP	SD	Source
Beaver pond (UV)	Tiger Salamander (<i>A. m. nebulosum</i>)	42–86	Ephemeroptera, Zooplankton, Diptera	2.85	0.03	This study
Beaver pond (MV)		167–176	Ephemeroptera, Hemiptera	3.66	0.05	
		48–63	Ephemeroptera, Zooplankton, Diptera	2.9	0.05	
Beaver pond (Wyoming)	Brook Trout (<i>Salvelinus fontinalis</i>) (fork length)	67	Ephemeroptera, Diptera	—	—	Allen and Claussen, 1960
		150	Ephemeroptera, Coleoptera, Diptera	—	—	
		186	Ephemeroptera, Coleoptera, Diptera	—	—	
Beaver pond (Idaho)	Brook Trout (<i>S. fontinalis</i>)	121–281	Diptera, Terrestrial, Trichoptera	—	—	Hilderbrand and Kershner, 2004
	Cutthroat trout (<i>O. clarki</i>) (total length)	95–266	Diptera, Terrestrial, Trichoptera	—	—	
Small lakes (Canada)	Brook Trout (<i>S. fontinalis</i>) (fork length)	<250	Zooplankton, Ephemeroptera, Diptera, Trichoptera, Odonata, Fish	3.4–3.8	—	Browne and Rasmussen, 2011
		>400	Fish	4.23	0.07	
Small lakes (Canada)	Brook Trout (<i>S. fontinalis</i>) (total length)	100–350	Benthic predatory macroinvertebrates, Zooplankton	4.08	0.14	Glaz et al., 2012
Large lake (Norway)	Brown Trout (<i>Salmo trutta</i>) (total length)	<150	Benthic invertebrates, Fish	3.59	0.21	Jensen et al., 2012
		>350	Fish	4.15	0.14	

complementarity of the two predators as invertebrate communities may vary in the presence of each via differential predation rates as well as indirect behavioral effects.

The results of this study suggest that functional complementarity of salamander larvae and salmonids in streams may differ widely from pond to pond, and depends both on predator size structure and the evolutionary history of available prey. Larval salamanders, with diets consisting of invertebrate prey, would only be complementary to smaller size classes of salmonids, and not larger, piscivorous size classes. Although salamanders and salmonids share overlapping prey resources, the behavioral responses of prey may differ widely between the two predator groups, altering community composition in the presence of each species and decreasing complementarity. Additionally, colonization of *A. m. nebulosum* is restricted to impounded reaches of stream ecosystems, limiting their impact on stream communities as a top predator, particularly in flowing reaches where salmonids have been shown to be important drivers of community structure (Power, 1992; Konishi et al., 2001). Thus, these findings suggest that although both *A. m. nebulosum* and salmonids are generalist top predators in stream ecosystems, *A. m. nebulosum* would be a complementary predator to salmonids in only a narrow range of conditions.

On a broader scale, this research supports previous work that has found functional redundancy or complementarity to exist under a limited range of environmental conditions (Wellnitz and Poff, 2001; Schmera et al., 2012). This study

highlights the importance of testing for functional complementarity over a range of environmental conditions as niche overlap between species may change, reducing the “insurance” of functional complementarity. Evaluating how predators differentially affect ecosystem function, rather than just community structure, would give a broader sense of the complementarity of the predators and enhance the utility of functional complementarity for the management of degraded ecosystems. Differences in ecosystem processes were outside the scope of this study, but are perhaps even more important than dietary niche in evaluating functional complementarity for management, particularly when broad services of an ecosystem are the goal of conservation rather than the protection of a subset of community members such as sport fish (Rosenfeld, 2002).

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