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# Coexistence in streams: do source–sink dynamics allow salamanders to persist with fish predators?

Adam J. Sepulveda · Winsor H. Lowe

**Abstract** Theory suggests that source–sink dynamics can allow coexistence of intraguild predators and prey, but empirical evidence for this coexistence mechanism is limited. We used capture–mark–recapture, genetic methods, and stable isotopes to test whether source–sink dynamics promote coexistence between stream fishes, the intraguild predator, and stream salamanders (*Dicamptodon aterrimus*), the intraguild prey. Salamander populations from upstream reaches without fish were predicted to maintain or supplement sink populations in downstream reaches with fish. We found instead that downstream reaches with fish were not sinks even though fish consumed salamander larvae—apparent survival, recruitment, and population growth rate did not differ between upstream and downstream reaches. There was also no difference between upstream and downstream reaches in net emigration. We did find that *D. aterrimus* moved frequently along streams, but believe that this is a response to seasonal habitat changes rather than intraguild predation. Our study provides empirical evidence that local-scale mechanisms are more important than dispersal dynamics to coexistence of streams salamanders and fish. More broadly, it shows the value of empirical data on dispersal and gene flow for distinguishing between local and spatial mechanisms of coexistence.

**Keywords** *Dicamptodon aterrimus* · Genetics · Capture–mark–recapture · Salamander · Stable isotope

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## Introduction

Intraguild predation, defined as predator–prey interactions among consumers that share the same trophic level (Holt and Polis 1997), is ubiquitous in aquatic and terrestrial systems (Werner and Gilliam 1984). However, the mechanisms that enable coexistence among intraguild predators and prey are poorly understood and rarely tested at the population level in the field. Theory predicts that coexistence is possible when intraguild prey are better competitors for a single, shared resource (Holt and Polis 1997), but empirical observations demonstrate coexistence occurs even when predators are better competitors (Navarrete et al. 2000). Because the combined effects of predation and competition are non-intuitive, yet can have large influences on the structure and function of natural communities (Polis et al. 1989), isolating the mechanisms that allow for coexistence of intraguild predators and prey is critical to advancing community ecology.

Empirical tests of intraguild coexistence have generally focused on local mechanisms, but models indicate that

asymmetric dispersal between spatially heterogeneous patches can allow local coexistence of inferior prey via source–sink dynamics (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002). Source populations are self-sustaining and produce surplus individuals that disperse to other populations. Continued immigration from a source is necessary to maintain inferior prey in sinks (Holt 1985; Pulliam 1988). Local coexistence via source–sink dynamics depends on the inferior prey having a competitive advantage in the source, or on the superior predator being unable to invade the source (Amarasekare 2003). Although models and mesocosm experiments suggest that coexistence via source–sink dynamics is possible (Amarasekare 2000; Amarasekare and Nisbet 2001), empirical tests in natural populations are limited because they are difficult to conduct.

The best method for testing local coexistence via source–sink dynamics is to eliminate dispersal and determine whether the prey species goes extinct in the sink (Diffendorfer 1998), but this method is impractical in most natural systems. Consequently, information on patch-specific vital rates and dispersal rates among patches is needed to operationally classify sources and sinks and to assess the contribution of dispersal to local coexistence in the sink (Runge et al. 2006). Without dispersal data, it is hard to infer source–sink dynamics because organisms that disappear from the study area are assumed to have died, when in reality some may be emigrants (Peery et al. 2006; Runge et al. 2006). Yet many empirical studies of source–sink dynamics present little or no dispersal data because estimating dispersal rates among patches is difficult (Diffendorfer 1998; Runge et al. 2006).

Systems where it is possible to collect direct data on dispersal are great resources for understanding source–sink dynamics. In most terrestrial habitats, recapture of marked individuals is challenging because the arena for dispersal is a two-dimensional, infinite plane (Kareiva 1983). Consequently, the effects of dispersal on population and community dynamics in these systems are inferred from indirect data, such as spatial and temporal variation in community composition. In headwater streams where critical resources are confined to stream channels, dispersal is easier to estimate (Grant et al. 2007). By using stream systems to test the role of dispersal in species coexistence directly, we can advance general empirical understanding of the community consequences of source–sink dynamics.

A major challenge in estimating dispersal, or more precisely immigration and emigration, arises from the fact that not all movers contribute demographically to the population where they settle (Lowe and Allendorf 2010). Moreover, field estimates are constrained by the timing and extent of sampling (Koenig et al. 1996). Patterns of genetic divergence provide information on dispersal over multiple generations (Wright 1951), and genetic assignment tests can detect immigrants from sites that were and were not sampled (Manel et al. 2005). Genetic structure has been detected at small spatial scales in many stream organisms (Spruell et al. 1999; Lowe et al. 2006), further justifying this approach as a complement to direct estimates of dispersal.

We used mark–recapture and genetic methods to test whether source–sink dynamics promote coexistence between stream salamanders and fish. Stream salamanders are the top predators in fishless, headwater streams in many parts of North America (Davic and Welsh 2004; Barr and Babbitt 2007). In streams with fish, salamanders become intraguild prey (Petranka 1983; Huang and Sih 1991; Barr and Babbitt 2007). Because fish prey on and outcompete stream salamanders (Petranka 1983; Resetarits 1991; Barr and Babbitt 2007), theory predicts that coexistence is not likely, yet stream salamanders and fish often co-occur in the same reach. Salamanders, however, also occupy headwater stream reaches that fish are unable to access because of movement barriers such as waterfalls (Storfer and Sih 1998; Barr and Babbitt 2007). Salamander dispersal from these upper, fishless reaches to lower reaches with fish has been suggested as a mechanism for coexistence with fish (Petranka 1983; Thiesmeier and Schuhmacher 1990; Resetarits 1995), but this mechanism has not been tested.

We assessed the contribution of dispersal to local population dynamics of a stream salamander, *Dicamptodon aterrimus*, in stream reaches with and without salmonid fish (*Oncorhynchus* sp. and *Salvelinus* sp.). Larvae of this salamander are strictly aquatic and adults are highly aquatic so movement is confined primarily to stream channels (Mullen et al. 2010). *Dicamptodon* species and fish feed primarily on stream macroinvertebrates, but fish also consume salamander larvae (Parker 1991; Rundio and Olson 2003). To test source–sink dynamics as a coexistence mechanism, we used capture–mark–recapture methods to estimate net movement rates, apparent survival ($\varphi$), recruitment ($f$), and realized population growth rate ($\lambda$) of *D. aterrimus* in upstream reaches without fish and downstream reaches with fish. We predicted that (1) net movement of *D. aterrimus* in upstream reaches would be downstream, (2) survival in fishless reaches would be greater than in reaches with fish, (3) local reproduction in reaches without fish would be greater than in reaches with fish, and (4) population growth would be $\geq 1$ for fishless reaches. To test our assumption that *D. aterrimus* are intraguild prey of fish, we used carbon and nitrogen stable isotopes to characterize fish consumption of *D. aterrimus*.

## Materials and methods

### Study system

*Dicamptodon aterrimus* is a large salamander (≤220 mm snout–vent length) found in streams and rivers in the Rocky Mountains of northern and central Idaho and western Montana (Stebbins 2003). This species exhibits facultative paedomorphosis, a polymorphism that results in the coexistence of gilled, fully aquatic adults and terrestrial, metamorphic adults in the same populations. Aquatic individuals of this genus feed primarily on stream insects in the drift and benthos, but larger salamanders can consume fish and smaller salamanders (Parker 1994). This species has broad habitat requirements within streams and frequently occurs with fish (Sepulveda and Lowe 2009).

We conducted this study in four headwater streams in the Lochsa River basin of the Clearwater River in eastern Idaho, USA (Online Resource 1). Our primary analysis focused on comparisons within and between Pondosa Creek and Pagoda Creek within the Fish Creek drainage. To assess the generality of our results from these two streams, we also investigated salamander movement and demography in two additional headwater streams without names, hereafter referred to as Stream 1 and Stream 2. Stream 1 and Stream 2 were tributaries of Post Office Creek, which drains into the Lochsa River 30 km upstream from the mouth of Fish Creek. These 4 streams were the only streams out of 40 surveyed with *D. aterrimus* abundances high enough for capture–mark–recapture estimates, and that matched our predator–prey coexistence criteria. Because of their proximity and similar geology, the four streams have similar physical habitat (Sepulveda and Lowe 2009). In this area, most precipitation falls as snow and stream flows peak during spring, reaching their lowest point from July to October. Multiple predatory fish species occur in headwater streams of this region, including bull trout (*S. confluentus*), steelhead and rainbow trout (*O. mykiss*), and westslope cutthroat trout (*O. clarkii lewisi*). Amphibian species include *D. aterrimus* and Rocky Mountain tailed frogs (*Ascaphus montanus*).

To test whether source–sink dynamics promote coexistence between *D. aterrimus* and fish, we used natural variation in the occurrence and density of *D. aterrimus* and salmonid fishes in these headwater streams (Online Resource 2). Within each stream, we sampled two 100-m reaches separated by 200 m of stream length. The lower and upper reaches of all sampled streams had *D. aterrimus*, but fish presence varied within and among streams. In Pondosa Creek and Stream 1, the lower reaches had fish ($\approx 0.20$ fish/m$^2$) and the upper reaches did not. Pagoda Creek had no fish and Stream 2 had fish ($\approx 0.40$ fish/m$^2$) in the lower and upper reaches. Waterfalls prevent fish from moving into Pagoda Creek and the upper reaches of Pondosa Creek and Stream 1. We were able to examine evidence for source–sink dynamics across this variation in co-occurrence.

### Capture–mark–recapture survey methods

To sample salamanders, we used Pollock's robust design (Pollock 1982) with 5 primary sampling periods in Pondosa Creek and Pagoda Creek and 4 primary sampling periods in Stream 1 and 2. In Pondosa Creek and Pagoda Creek, the primary sampling periods were August 2006, July 2007, August 2007, July 2008, and August 2008. During each primary sampling period, secondary samples occurred 24 h apart. Sampling was the same in Stream 1 and 2, but these streams were not sampled in August 2006. We used a backpack electrofisher (Smith-Root, LR-24, smooth DC with 400–520 V) to search for aquatic larval and adult salamanders, standardizing effort across surveys by time. We did not survey for *D. aterrimus* terrestrial adults in the riparian area because they are cryptic and rare (J. Sauder, Idaho Fish and Game, personal communication) and overland movement between streams is minimal (Mullen et al. 2010); therefore, our demographic rates pertain only to aquatic *D. aterrimus*.

The longitudinal position (distance from the confluence, m), snout–vent length (SVL, mm), and mass (mg) of all individuals encountered were recorded. All unmarked salamanders were individually marked using fluorescent elastomer (Northwest Marine Technologies, Shaw Island, WA, USA) and marked individuals were recorded. In previous studies, retention of these marks was high throughout the life of amphibians (Grant 2008). Sex was not recorded because these salamanders cannot be sexed in the field non-lethally.

### Movement direction

To test if net movement (defined as the difference between immigration and emigration) in upstream reaches was downstream-biased and greater than net movement in downstream reaches with fish, we described *D. aterrimus* movement across all primary sampling periods both within and between stream reaches. Movement of recaptured individuals was measured as distance along the stream (m) from the position of last capture. To quantify movement, we used frequency distributions of distances moved, assigning negative values to downstream moves and positive values to upstream moves. To determine if salamander movement distributions were consistent between the two reaches within each stream, we tested for differences in the movement distribution of the two study reaches using a Kolmogorov–Smirnov test. We assessed directional bias by

testing for skewness of the movement distribution (Zar 1984). To better understand if salamander × fish coexistence in downstream reaches was influenced by size-biased movement rather than movement rate, we tested whether distance moved and directional bias were linked to salamander size (SVL) using Spearman rank correlation analyses and $t$ tests.

### Apparent survival, population growth rate, and recruitment

To assess how fish affected local population dynamics of *D. aterrimus*, we modeled variability in apparent survival ($\varphi$) and realized population growth rate ($\lambda$) by stream reach and time using the robust design Pradel (Huggins closed capture) model in program MARK (Pollock and Otto 1983; Pradel 1996; White and Burnham 1999). Because Pradel models assume demographic closure and therefore cannot incorporate transitions between populations, individuals that dispersed between reaches had two recapture histories, each specific to a reach. We chose not to use a multistrata model because our sampling reaches were not continuous and because we observed very low rates of movement between reaches.

The primary parameters of interest were $\varphi$ and $\lambda$, so we first evaluated models of capture probability ($p$) and recapture probability ($c$) to avoid unnecessary bias and imprecision in the $\varphi$ and $\lambda$ estimates (Lebreton et al. 1992). To identify the best model of $p$ and $c$ for each stream, we paired the global model for $\varphi$ and $\lambda$ with all possible combinations of $p \neq c$ and $p = c$. Because primary sampling periods occurred in July and August of each year, we specified time as unequal intervals between primary occasions. The global model of $\varphi$ and $\lambda$ always varied by reach, primary sampling period and time, whereas all possible combinations of $p \neq c$ and $p = c$ also included models that did not vary by reach, primary, sampling period, or time. This structure resulted in eight combinations of $p \neq c$ and eight combinations of $p = c$.

Both $\varphi$ and $\lambda$ were assumed to be constant over secondary samples, but we assumed that they varied across primary sampling periods because of seasonal changes in stream habitat within and among years. To test the predictions that apparent survival ($\varphi$) was lower in reaches with fish than in fishless reaches, and that realized population growth rate ($\lambda$) did not differ between reaches with and without fish, we modeled variability in $\varphi$ and $\lambda$ by stream reach (r). We used Program MARK to compare five models. In Model 1, $\varphi$ and $\lambda$ varied by reach. In Model 2, $\varphi$ varied by reach and $\lambda$ was constant. In Model 3, $\varphi$ was constant and $\lambda$ varied by reach. In Model 4, $\varphi$ and $\lambda$ were constant. In Model 5, we compared the top-ranked model from Models 1–4 to the same model with no variation

across primary sampling periods. Estimation of $\varphi$ and $\lambda$ allowed for the estimation of recruitment ($f$) for all tested models because

$$f_t = \lambda_t - \varphi_t$$

in the Pradel model (Runge et al. 2006), where $f_t$ is the number of new individuals entering the population in year $t + 1$ per individual in the population in year $t$.

We ranked competing models according to how well they were supported by the capture data using Akaike's Information Criterion for small sample size ($AIC_c$), $AIC_c$ weights, and evidence ratios (Burnham and Anderson 2002). Parameter estimates were calculated using model averaging for Pondosa Creek and Pagoda Creek (Burnham and Anderson 2002). We tested the goodness-of-fit of the model with the most parameters (Model 1) using program U-CARE 2.2 (Choquet et al. 2005). Because the temporal scale of surveys and number of individuals sampled in Stream 1 and 2 were lower than in Pondosa Creek and Pagoda Creek, we used program MARK only to compare multiple hypotheses and not to estimate parameter values in those streams.

### Genetic assessment of movement and population structure

To complement our direct, empirical estimates of movement, we used genetic methods to estimate gene flow between reaches within each stream. A small section of tail tissue was clipped from 17–20 captured salamanders in each stream reach in July 2007 and stored in 95% ethanol. Both juveniles and adult salamanders were sampled. SVL of sampled animals ranged from 22 to 180 mm and weights ranged from <1 to 140 g.

Samples were genotyped at 9 microsatellite loci (D04, D06, D08, D13, D14, D15, D18, D24, Dte6) developed for *Dicamptodon tenebrosus* and *D. copei* (Curtis and Taylor 2000; Steele et al. 2008). Methods for DNA extraction, amplification, and visualization are described in Mullen et al. (2010). We tested for significant departures from Hardy–Weinberg (HW) proportions and gametic disequilibrium using exact tests implemented in GENEPOP version 4.0 (Raymond and Rousset 1995).

We calculated genetic differentiation with pairwise $F_{st}$ (GENEPOP; Raymond and Rousset 1995) and used these $F_{st}$ values to assess levels of divergence occurring between stream reaches. We also tested for population differentiation between stream reach pairs based on distribution of alleles using Fisher's exact tests (GENEPOP; Raymond and Rousset 1995). We used partial Bayesian individual assignment tests (Rannala and Mountain 1997) within each stream to classify individuals to either the downstream or upstream reach based on the expected frequency of an

individual's multilocus genotype in each reach (GENE-CLASS2; Piry et al. 2004). Individuals were assigned to the inferred genetic population for which they had the highest membership value (estimated as a probability). We used high and moderate thresholds to identify residents and immigrants ($p \geq 95$ vs. 75%). Residents were individuals that assigned to the stream reach from which they were sampled, while immigrants were individuals that assigned to the alternative stream reach. We used Pearson correlation to compare the proportion of residents based on $\geq 75$ and $\geq 95\%$ assignment thresholds. To assess movement direction bias, we compared the proportion of immigrants captured at the downstream reach to the proportion of immigrants captured at the upstream reach.

### Fish consumption of *D. aterrimus*

To test the assumption that *D. aterrimus* are intraguild prey of fish, we used stable isotopes of carbon ($^{13}C{:}^{12}C$, expressed as $\delta^{13}C$) and nitrogen ($^{15}N{:}^{14}N$, expressed as $\delta^{15}N$) to quantify the relative contribution of different prey resources to fish predators. Used together, $\delta^{13}C$ and $\delta^{15}N$ reflect temporally integrated data on an individual's diet, which are difficult to compile with stomach data alone (Sepulveda et al. 2009). Within each 100-m reach in 2007, we collected stable isotope samples from a small piece of tail clipped from each salamander (Simon et al. 2003) and from white muscle below the dorsal fin of each fish (Sepulveda et al. 2009). We sampled larval and aquatic adult salamanders, but not terrestrial adult salamanders because they rarely occur in the stream with fish. To quantify the contribution of major prey sources to fish diets, we collected stable isotope samples from stream-conditioned leaves of terrestrial vegetation, epilithic organic matter, aquatic invertebrates, *A. montanus* larvae, and terrestrial invertebrates in July and August 2007. All samples were stored on ice in the field and then frozen until processed.

We dried samples for 48 h at 65°C. All samples were ground to a fine powder and packed in $4 \times 6$ mm tin capsules (Costech Analytical Technologies, Valencia, CA, USA). $\delta^{13}C$ and $\delta^{15}N$ were measured using a Thermo Scientific Delta V Advantage mass spectrometer coupled with a Costech ECS 4010 elemental analyzer via a Conflo IV gas interface and the Smithsonian Institution OUSS/MCI Stable Isotope Mass Spectrometry Facility (Suitland, MD, USA). We reported all stable isotope values in the $\delta$ notation where $\delta^{13}C$ and $\delta^{15}N = ([R_{sample}/R_{standard}]-1)\ 1{,}000$, where R is $^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$. The global standard for $\delta^{13}C$ is Vienna PeeDee Belemnite and for $\delta^{15}N$ is atmospheric nitrogen. All runs included a set of standards for every 10 samples. Standards include USGS40 (L-glutamic acid), USGS41 (L-glutamic acid), and Costech acetanilide. The reproducibility of standards during individual runs was no

greater than $\pm 0.2\permil$ ($1\sigma$) for both $\delta^{13}C$ and $\delta^{15}N$, all sample data were therefore considered to have an associated error of $\pm 0.2\permil$. The reproducibility of replicate salamander ($n = 20$) and fish ($n = 5$) samples we ran throughout this analysis was $0.25\permil$ ($1\sigma$) for $\delta^{13}C$ and $0.19\permil$ ($1\sigma$) for $\delta^{15}N$. We used individual $\delta$ values to estimate reach averages for salamanders and fish.

To describe the food resources that fish assimilated, we used IsoSource 1.3 software (Phillips and Gregg 2003). We assigned prey sources into six categories: aquatic non-predators (shredders and grazers), aquatic predators (collector–gatherers and predators), terrestrial invertebrates, *A. montanus* larvae, salmonid juveniles (<60 mm total length), and *D. aterrimus* larvae (<60 mm snout–vent length). We used multiple discriminant function analyses to test if the assignments of individuals into our six prey categories were isotopically distinct for each stream reach. Because we found that $\geq 90\%$ of our samples were re-classified correctly, we used these six prey categories for all diet analyses. We corrected prey isotope values for trophic enrichment using the widely-accepted values of 1 and $3.4\permil$ for $\delta^{13}C$ and $\delta^{15}N$, respectively (e.g., Post 2002; Decottignies et al. 2007). We used the means of prey isotope values from each stream reach to estimate the proportional contribution of each prey source to fish consumers. The source increment was set at 1%. Tolerance was initially set at $0.01\permil$, but we incrementally increased the tolerance value by $0.05\permil$, up to a maximum of $0.5\permil$, if the mixture isotope values were outside the polygon delineated by the six prey sources. Following Phillips and Gregg (2003), we recorded the range (1st–99th percentile) and mean feasible dietary contributions of each prey source for each consumer entered into IsoSource simulations. Low maxima (99th percentile) from IsoSource simulations indicate that a prey source can be rejected as important, while relatively high minima indicate that the source may be important. Large ranges between minima and maxima are not informative unless the minimum is relatively high (Phillips and Gregg 2003; Benstead et al. 2006).

## Results

### Reach surveys

Over the 3-year study, we marked 232 individuals in Pondosa Creek and 295 individuals in Pagoda Creek and recaptured 49 and 39% of these individuals, respectively, one or more times (Table 1). Over 2 years, we marked 73 individuals in Stream 1 and 108 individuals in Stream 2 and recaptured 32 and 29% of these individuals, respectively, one or more times (Table 1). Movement between stream reaches was rare. Only three individuals (3%)

**Table 1** Mean *Dicamptodon aterrimus* closed population estimate ($\hat{N}$) over five primary sessions from the best-supported Pradel-Robust design model, the number of unique *Dicamptodon aterrimus* individuals captured, the number of individuals recaptured, and the recapture rate ($\hat{p}$) for each stream reach sampled in Pondosa Creek and Pagoda Creek, 2006–2008 and Stream 1 and Stream 2, 2007–2008

| Reach | $\hat{N}$ (mean ± 1SE) | Total captures | No. captured | No. recaptured | $\hat{p}$ |
|---|---|---|---|---|---|
| Pondosa | | | | | |
| Low | 40 ± 5 | 244 | 127 | 62 | 0.49 |
| Up | 36 ± 5 | 201 | 105 | 51 | 0.49 |
| Pagoda | | | | | |
| Low | 48 ± 3 | 210 | 161 | 67 | 0.42 |
| Up | 54 ± 9 | 188 | 134 | 48 | 0.36 |
| Stream 1 | | | | | |
| Low | 27 ± 4 | 78 | 43 | 15 | 0.35 |
| Up | 23 ± 5 | 62 | 30 | 17 | 0.57 |
| Stream 2 | | | | | |
| Low | 76 ± 14 | 80 | 46 | 22 | 0.48 |
| Up | 102 ± 11 | 97 | 62 | 26 | 0.42 |

originally marked in the upper reach of Pondosa Creek were later captured in the lower reach, and one individual (2%) originally marked in the upper reach of Pagoda Creek was later captured in the lower reach. One individual (3%) originally marked in the upper reach of Stream 1 was later captured in the lower reach and no recaptured individuals moved between reaches in Stream 2. Across all four streams, we recaptured no individuals in the upper reaches that were originally marked in the lower reaches.

Analysis of movement direction

Directional movement bias differed between streams with and without fish but was similar between the upper and lower reaches of each stream (Kolmogorov–Smirnov tests: $P > 0.05$) so we pooled data across reaches within each stream (Fig. 1). In Pondosa Creek (fish in the lower reach, fishless in the upper reach), *Dicamptodon aterrimus* had a downstream bias in movement [skewness $= -0.72 \pm 0.26$, $n = 115$, $P$ (skewness $= 0$) $< 0.05$]. In Pagoda Creek (without fish), individuals had no directional movement bias (skewness $= 0.19 \pm 0.29$, $n = 70$, $P > 0.20$).

Distance moved was not correlated with individual size (SVL) in either stream (Spearman rank correlation: Pondosa: $R_s = -0.17$, $n = 87$, $P = 0.12$ and Pagoda: $R_s = -0.06$, $n = 70$, $P = 0.61$). However, individuals that moved upstream were larger (SVL) than those that moved downstream in Pondosa Creek (*t* test: $t = -2.26$, $df = 85$, $P = 0.03$) and Pagoda Creek (*t* test: $t = -2.49$, $df = 68$, $P = 0.02$).

Individuals in Streams 1 and 2 had no directional movement bias (Stream 1: skewness $= -0.80$, $n = 23$, $P > 0.05$; Stream 2: skewness $= -0.22 \pm 0.44$, $n = 31$,
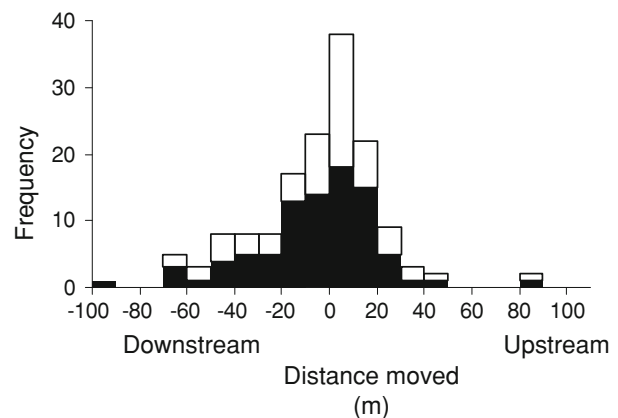


**Fig. 1** Distribution of *D. aterrimus* individuals recaptured in Pagoda Creek (*open bars*) and Pondosa Creek (*filled bars*), Idaho, USA; $n = 157$. Positive values represent upstream moves and negative values represent downstream moves. Data are pooled over all recaptured intervals and between reaches within each stream

$P > 0.20$) and distance moved was not correlated with individual size in either stream (Spearman rank correlation: Stream 1 $R_s = 0.15$, $n = 23$, $P = 0.49$, and Stream 2 $R_s = -0.23$, $n = 31$, $P = 0.21$). Direction of movement (upstream or downstream) was also not correlated with individual size (*t* test: Stream 1 $t = -0.67$, $df = 21$, $P = 0.51$; Stream 2 $t = -1.44$, $df = 29$, $P = 0.16$).

Demography

The goodness-of-fit tests were not significant ($\chi^2 > 64.74$, $P > 0.09$) and showed no sign of transience ($z = 1.42$, 2-sided test, $P > 0.21$) or of trap-response ($z > -1.53$, 2-sided test, $P > 0.12$), suggesting that the model with the

most parameters from each stream (Model 1) fit the data well. We then compared Model 1 to the other four reduced-parameter models. In the best-fitting model, $\varphi$ and $\lambda$ did not differ between upper and lower stream reaches within any stream (Online Resource 3). Apparent survival and $\lambda$ varied across time in Pondosa Creek, but were constant in Pagoda Creek, Stream 1, and Stream 2 (Online Resource 3). However, models with time-variant $\varphi$ and $\lambda$ were also plausible in Streams 1 and 2. Because recruitment $(f) = \lambda - \varphi$ in the Pradel model, and because $\varphi$ and $\lambda$ did not differ between reaches within each stream, we can conclude that recruitment did not differ between reaches within each stream.

Standard error estimates of $\varphi$ and $\lambda$ obtained by model averaging overlapped between reaches and across streams (Fig. 2). Apparent monthly survival between primary sessions ranged from 0.71 to 0.82 in Pondosa Creek and 0.62 to 0.71 in Pagoda Creek. Realized population growth rate between primary sessions ranged from 0.77 to 1.56 in Pondosa Creek and 1.01 to 1.08 in Pagoda Creek.

Gene flow and population structure

All stream reaches were in Hardy–Weinberg equilibrium ($P > 0.05$). Only 8% of 288 tests for linkage disequilibrium were significant ($P < 0.05$), but the identity of non-randomly associated loci varied across stream reaches and no comparisons were significant after sequential Bonferroni correction for multiple tests (Rice 1989).

In all streams, $F_{st}$ estimates were less than 0.10 (Table 2). Pondosa Creek had the highest $F_{st}$ value, while Stream 1 and Stream 2 had $F_{st}$ estimates that approached 0. Genetic differentiation between Pondosa Creek reaches was significant (Fisher's exact test: $\chi^2 = 59.74$, $P < 0.001$), but all other reach pairs did not differ ($\chi^2 < 23.58$, $P > 0.17$).

Individual assignment tests supported our genetic differentiation results (Table 2). We found significant population structure only in Pondosa Creek, where the majority of individuals were assigned to the reach from which they were sampled (i.e., residents) and few individuals were assigned to the alternate reach (i.e., immigrants). In all other streams, <47% of individuals were assigned as residents and as many as 42% were assigned as immigrants. Assignment results of residents based on moderate ($\geq75\%$) and high ($\geq95\%$) thresholds were strongly correlated (Pearson correlation: $r = 0.86$, $df = 8$), but immigrant assignments were not correlated ($r = 0.41$, $df = 8$). Assignment of immigrants based on the 95% threshold were 67–100% lower than assignments based on the 75% threshold in 7 of 8 stream reaches. Only the proportion of immigrant assignments in the lower reach of Pondosa Creek did not vary by threshold stringency. Directional bias of immigration varied across streams. Pondosa Creek and Stream 1 had little support for any directional bias, but the majority of individuals assigned as immigrants moved downstream in Pagoda Creek and Stream 2.

Fish consumption of D. aterrimus

We found that fish had high inter-individual diet variability and that all fish populations were generalists that consumed



**Fig. 2** Estimates (±95% C.I.) of **a**, **b** apparent survival and **c**, **d** realized population growth rate ($\lambda$) of *Dicamptodon aterrimus* in the lower reach (*filled bars*) and upper reach (*open bars*) of Pondosa Creek (**a**, **c**) and Pagoda Creek (**b**, **d**) between five primary sampling sessions (*1* August 2006, *2* July 2007, *3* August 2007, *4* July 2008, *5* August 2008). Estimates are model averages taken from all fitted robust design models
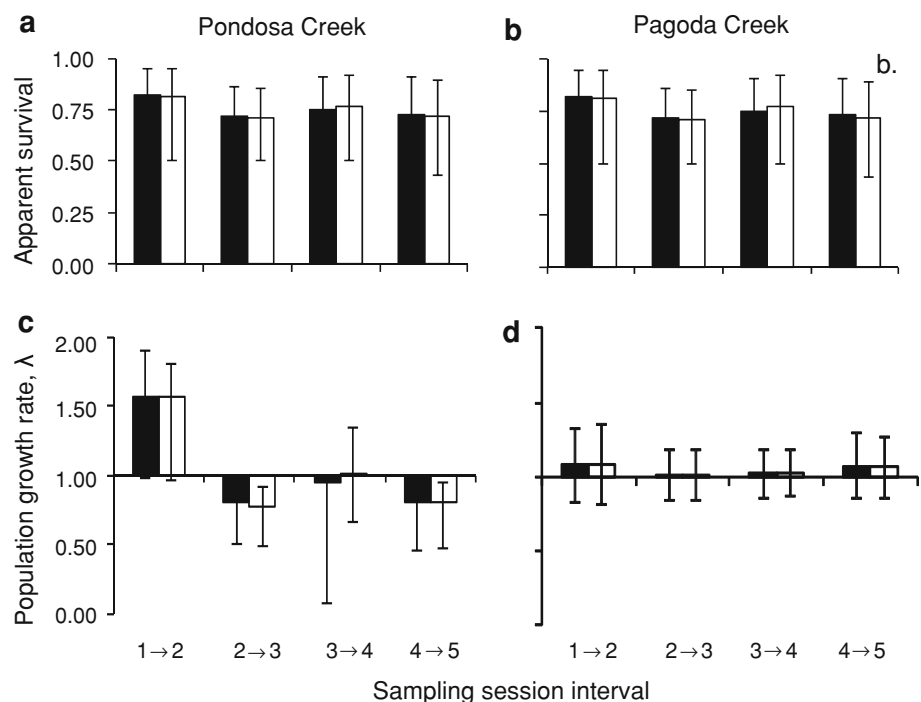
**Table 2** Sample size ($n$), genetic differentiation ($F_{st} \pm 1$ standard error), and the proportion of *Dicamptodon aterrimus* individuals assigned as residents or immigrants

| Stream | Reach | $n$ | $F_{st}$ | $n$ | ≥75% Probability | | ≥95% Probability | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Resident | Immigrant | Resident | Immigrant |
| Pondosa | | | | | | | | |
| | Low | 18 | 0.06 ± 0.02 | 18 | 0.73 | 0.06 | 0.72 | 0.06 |
| | Up | 17 | | 17 | 0.71 | 0.06 | 0.47 | 0.00 |
| Pagoda | | | | | | | | |
| | Low | 17 | 0.02 ± 0.01 | 17 | 0.41 | 0.35 | 0.24 | 0.12 |
| | Up | 18 | | 18 | 0.28 | 0.17 | 0.11 | 0.06 |
| Stream 1 | | | | | | | | |
| | Low | 18 | 0.01 ± 0.01 | 18 | 0.28 | 0.28 | 0.17 | 0.00 |
| | Up | 18 | | 18 | 0.06 | 0.33 | 0.00 | 0.00 |
| Stream 2 | | | | | | | | |
| | Low | 19 | 0.01 ± 0.01 | 19 | 0.47 | 0.42 | 0.05 | 0.11 |
| | Up | 18 | | 18 | 0.17 | 0.22 | 0.06 | 0.06 |

Genetic differentiation estimates are between the downstream and upstream reaches of four streams. Individuals were assigned as residents or immigrants in the downstream and upstream reaches of four streams based on a moderate probability (≥75%) and high probability (≥95%). Residents are individuals that assigned to the stream reach from which they were sampled, while immigrants are individuals that assigned to the alternative stream reach

a variety of prey items, including salamander larvae (Fig. 3). Only terrestrial invertebrates could be rejected as an important prey source for fish because the maximum was near 0%. Although salamander larvae were not the dominant prey item in fish diets, they comprised 19–49% of fish diets, supporting our assumption that *D. aterrimus* is an important intraguild prey of fish.
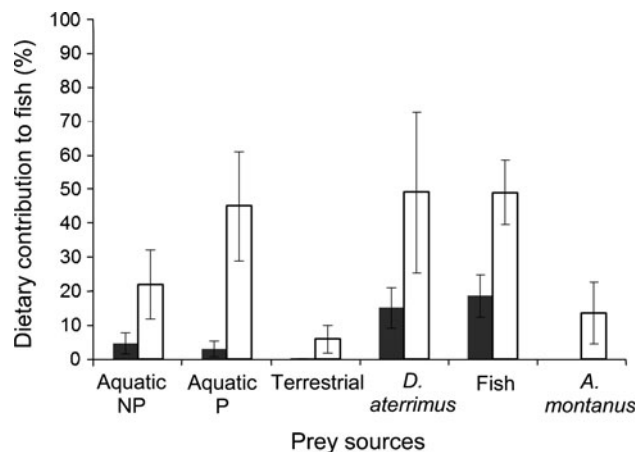


**Fig. 3** Percent dietary contribution (mean ± 95% C.I.) of prey sources to fish based on the 1st percentile minima (*filled bars*) and 99th percentile maxima (*open bars*) from IsoSource simulations: aquatic non-predators (*Aquatic NP*), aquatic predators (*Aquatic P*), terrestrial, *D. aterrimus*, fish, and *A. montanus*. Percent contributions do not sum to 100% because these are minimas and maximas

## Discussion

We used direct and indirect methods to test whether source–sink dynamics promote coexistence between salamanders and fish in headwater streams. Our results suggest that stream reaches with fish are not population sinks for *D. aterrimus*, even though fish consume salamanders, and that salamander movement between stream reaches is not the primary mechanism for *D. aterrimus* × fish coexistence. Apparent survival, recruitment, and population growth rates did not differ between reaches within streams. Because there was no difference in net emigration between upstream and downstream reaches, we conclude that population growth was a function of local survival and recruitment but not movement. Although movement did not influence population growth rates or coexistence with fish, we did find that *D. aterrimus* movement and gene flow within and between stream reaches was common.

Accurate identification of source–sink dynamics using direct, capture–mark–recapture field data are rare because classification of subpopulations as sources and sinks requires data on within- and among-population vital rates (Diffendorfer 1998; Peery et al. 2006; Runge et al. 2006). Most mark–recapture studies, including ours, estimate apparent survival, the probability of surviving and staying within a local population, and not true survival. If only estimates of recruitment and apparent survival are used, then subpopulations that export many individuals may be considered sinks because emigrants are recorded as

mortalities (Runge et al. 2006). In our study, we used multiple lines of inference to overcome this problem and assess whether upstream subpopulations serve as potential sources.

First, we found that all sampled subpopulations were potential sources because $\lambda$ estimates overlapped 1. Because apparent survival is $\leq$ true survival, emigration from a reach would not change our classification of all sampled reaches as sources. Second, we compared frequency distributions of distances moved and found no difference in net emigration between upstream and downstream reaches in all streams—that is, salamanders moving into each downstream reach were balanced by those leaving. Third, we used Runge et al.'s (2006) contribution metric to distinguish sources and sinks. The contribution metric ($C^r$) is the per capita contribution of a member of the focal subpopulation to the larger population and is estimated as:

$$C^r = \lambda^r_{loc} + E^r - I^r,$$

where $\lambda^r_{loc}$ is the local population growth rate in subpopulation $r$, $E^r$ is the emigration rate from $r$, and $I^r$ is the immigration rate into $r$. If $C^r > 1$, the subpopulation is a net contributor to the overall population and is therefore a source. If $C^r < 1$, the subpopulation is a sink. We found that $E^r \approx I^r$ and $\lambda^r_{loc} \geq 1$ for all sampled reaches with and without fish, therefore $C^r > 1$. Finally, individual assignment tests indicated that salamanders dispersed both upstream and downstream in all sampled reaches.

## Movement distance and frequency

Although salamander movement did not influence local population dynamics, we found that *D. aterrimus* movement was common and size-dependent. Of recaptured salamanders, 61% moved >10 m, and 4% moved >100 m. These movements apparently translated into high rates of gene flow between pairs of stream reaches (i.e., low $F_{st}$) and assignments of up to 42% of individuals sampled in a stream reach as immigrants.

Large salamanders were more likely to move upstream in Pondosa Creek and Pagoda Creek. It is unlikely that these size-dependent movement patterns resulted from passive displacement of smaller salamanders downstream due to flow, slope, or sampling because the variance of distance moved increased linearly with time (Online Resource 4). Cecala et al. (2009) also found that larger stream salamanders (*Pseudotriton rubber*) exhibited upstream-biased movement and that there was no evidence for passive downstream drift of smaller salamanders. As in many stream fishes, size-dependent movement could reflect ontogenetic differences in habitat needs (Werner and Gilliam 1984). The few salamanders that made longer

movements between stream reaches varied in size (42–101 mm SVL) and had similar body condition (length-corrected mass) to salamanders that did not leave the study reach (A. Sepulveda, unpublished data). Long-distance movements were recorded in all survey years and were not associated with population density (Online Resource 5) or specific disturbances, such as the low summer flows in 2007 or a large spring-runoff in 2008.

Previous studies found that most stream salamanders remain close to their origin, but that directional bias of movement varies among species (Barbour and Harvey 1969; Nussbaum and Tait 1977; Lowe 2003). Our results support these general patterns. We found that >95% of individuals remained within the stream reach of original capture and that directional bias varied among streams. However, shorter, within-reach movements were common in *D. aterrimus* (Fig. 1). This is very different from *Gyrinophilus porphyriticus*, another headwater salamander, where >50% of individuals recaptured over 3 years moved $\leq$1 m (Lowe 2003).

Despite the low number of observed movements between reaches, our low $F_{st}$ estimates suggest that dispersal between stream reaches does occur. However, assignment tests indicated that most immigrants were from stream reaches not sampled because few immigrants were assigned with a high probability ($\geq$95%) of belonging to the opposite stream reach. Along with our capture–mark–recapture data, these results suggest that immigrants were from stream reaches immediately above or below our sampled reaches, and that the degree of genetic differentiation between two stream reaches should increase with increasing separation (i.e., isolation-by-distance model). Recent research on *D. aterrimus* supports this prediction: Mullen et al. (2010) found that in-stream distance was a strong predictor of genetic divergence, and that this isolation-by-distance pattern was driven by limited migration.

What drives the frequent, short-distance movements in *D. aterrimus*? We suggest that the local-scale movement pattern of *D. aterrimus* is a response to the temporal and spatial variability in habitat quality that is typical of Rocky Mountain streams, where stream flows are snowmelt driven. Microhabitats in which we captured salamanders in July were often dry by August. It is likely that individuals move from poor to better microhabitats as stream flow decreases throughout the summer. Variability in abiotic stream conditions (e.g., temperature) has been linked to stream salamander movement patterns in other systems that receive frequent precipitation throughout the year (Cecala et al. 2009; Lowe 2009), but has not been tested in headwater streams that have extreme low flows like those in Lochsa River basin. Geographic variation in flow conditions may explain why our results differ from other data showing that short-distance movements are rare in stream

salamanders (Bruce 1986; Ferguson 1998; Lowe 2003; Grant et al. 2010). Most studies have occurred in the southeastern and northeastern United States, where habitat quality has less temporal variability because stream flow is stabilized by summer precipitation. We suggest specific recommendations for the conservation and management of *D. aterrimus* and other stream organisms in the Rocky Mountains should not be based on studies from other geographic regions. Overall, these results and previous findings (Sepulveda and Lowe 2009) suggest that *D. aterrimus* has many attributes that allow it to survive in exceptionally dynamic stream environments.

### Alternative mechanisms of coexistence

Our study provides compelling evidence that local mechanisms, and not spatial dynamics, promote coexistence of *D. aterrimus* and fish. In other systems, stream salamanders have evolved means of minimizing fish predation, including increased use of predator refugia (Sih et al. 1992), chemical deterrents (Brodie and Formanowicz 1987), and plasticity in behavior, tail color, and morphology (Van Buskirk and Schmidt 2000). Previous studies suggest that increased refuge use and chemical deterrents are unlikely mechanisms of *D. aterrimus* × fish coexistence. First, interstitial refuge availability was a poor predictor of *D. aterrimus* density in streams with and without fish (Sepulveda and Lowe 2009), and many salamanders were observed on top of stream substrate during the day. Second, our stable isotope diet analyses of *D. aterrimus* and previous research on *D. tenebrosus* indicate that they are eaten by stream fishes (Parker 1991; Rundio and Olson 2003). Future studies should test whether accelerated growth promotes coexistence with fish. Fish are gape-limited and only consume prey they can swallow whole (Werner 1977); therefore, salamanders with accelerated growth rates may have lower predation risk from gape-limited fish (Petranka 1983). Because salamanders, such as *D. aterrimus*, can grow larger than many resident fish in high-elevation streams, there is also a potential shift from intraguild prey to intraguild predator.

The issue of how prey coexist with their intraguild predators has received substantial attention in the last 20 years. Models of coexistence have advanced from simple competitive tradeoffs in a local patch to more complex models incorporating movement among patches, resource subsidies, and individual behavior (e.g., Arim and Marquet 2004; Amarasekare 2006). Our study provides empirical evidence that local-scale mechanisms within patches are more important than movement dynamics among patches to *D. aterrimus* × fish coexistence, despite active movement of salamanders along streams. Further empirical tests are needed to identify the specific local-scale mechanisms of coexistence. However, this research shows the value of empirical data on dispersal and gene flow for distinguishing between local and spatial mechanisms of coexistence.

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