

TROUT PREDATORS AND DEMOGRAPHIC SOURCES AND SINKS IN A MAYFLY METAPOPOPULATION

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Abstract. Habitat patches often differ in environmental conditions, and the degree of environmental heterogeneity among patches is thought to influence population dynamics at the regional (metapopulation) scale. In a previous study, I found evidence of a source–sink dynamic in a metapopulation of the mayfly *Callibaetis ferrugineus hageni* occupying beaver ponds with or without brook trout predators, where adult females frequently dispersed among ponds, and frequently oviposited in ponds with trout. Here, I tested the hypothesis that trout create habitat sinks by manipulating trout densities and estimating local population growth rates (λ) of *Callibaetis*. In addition, *Callibaetis* emergence rates were estimated in the mayfly generation before the manipulation. Among ponds, λ ranged from 0.062 to 2.631, and nine Monte Carlo simulations scenarios revealed that four ponds had λ significantly below replacement (sinks) while the presence of source ponds was less conclusive. The manipulation of trout did not result in a detectable treatment effect, perhaps because of low statistical power resulting from high within-treatment variation in trout densities. However, point estimates of λ and emergence rates were negatively and exponentially related to trout density, such that nearly all ponds with more than 1 trout/100 m² were sinks. Further, multiple regression analyses were consistent with the hypothesis that trout reduced λ and emergence rates, while other biotic and abiotic factors did not provide explanatory power. The results support the hypothesis that source–sink population dynamics may be common in freshwater habitats, and that prey metapopulation dynamics may be predicted from the distribution of predators, prey movement and habitat selection behaviors, and factors influencing the outcome of predator–prey interactions.

Key words: complex life cycle; dispersal; Ephemeroptera; habitat quality; metapopulation; predator–prey; source–sink; trout.

INTRODUCTION

The type of metapopulation dynamic displayed by a taxon is thought to depend strongly on the degree to which patches differ in environmental conditions, how organisms move among patches, and whether organisms can recognize and select suitable habitat (Harrison and Taylor 1997, Boughton 2000). In particular, variation in local population growth rate and constraints on dispersal may result in a source–sink dynamic (Pulliam 1988) where some individuals attempt development in habitat patches of low “quality”—sink patches with population growth rates below replacement. The persistence of populations in sink habitats is dependent on the net migration of individuals from source patches, where population growth rates are greater than replacement (e.g., $\lambda > 1$). While intuitively appealing, few empirical studies are available to assess whether source–sink dynamics are common in nature (Diffendorfer 1998, Thomas et al. 2001; but see Boughton

1999, Ferraras 2001, Johnson 2004). This paucity stems from the difficulty of collecting demographic parameter estimates and dispersal information for multiple populations (Hanski and Simberloff 1997, Harrison and Taylor 1997, Diffendorfer 1998, Thomas et al. 2001).

The complex life cycles possessed by many freshwater taxa coupled with the spatial structure of the habitat suggest the potential for metapopulations to be widespread in freshwater systems. In particular, lentic habitats are spatially discrete and are inhabited by many taxa with terrestrial adults that may move among habitat patches, such as aquatic insects and amphibians. Further, closely spaced water bodies frequently exhibit differences in community structure that may arise from differences in abiotic and biotic factors for individual taxa (e.g., Hall et al. 1970, McPeck 1989). Recent reviews suggest that pond drying and the presence or absence of fish predators have strong influences on local populations and communities (Batzer and Wissinger 1996, Wellborn et al. 1996, Batzer et al. 1999). Hence, aquatic organisms may encounter a mosaic of suitable and unsuitable habitat patches as they move through the landscape.

In previous studies, I examined a metapopulation of *Callibaetis ferrugineus hageni* Eaton mayflies (Caudill

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2003a, b, Caudill and Peckarsky 2003). Larvae developed in beaver ponds and adult females had the potential to disperse among ponds before oviposition. The studies revealed that (1) larvae did not exhibit adaptive behavioral or life history shifts in the presence of trout; (2) fewer adult mayflies emerged from ponds with trout; (3) females readily dispersed among ponds before ovipositing, but did not selectively oviposit with respect to the presence of trout predators; and (4) some ponds were net exporters of ovipositing females adults, while others were net importers. Taken together, the results were best explained by a source-sink dynamic model rather than other metapopulation models, and suggested that trout reduce local *Callibaetis* population growth rates.

Here, my aims were (1) to explicitly test for the presence of demographic sources and sinks in the *Callibaetis* metapopulation by estimating local population growth rate, λ_i , (2) to test experimentally whether trout negatively affected *Callibaetis* λ_i by manipulating trout densities, and (3) to examine how *Callibaetis* traits and the distribution of trout predators related to the observed metapopulation dynamic. I studied two generations of mayfly, where I estimated emergence to the adult stage for mayflies in beaver ponds prior to a manipulation of trout populations, and *Callibaetis* λ_i at each pond after the manipulation.

METHODS

The study system consisted of 12 beaver ponds near the Rocky Mountain Biological Laboratory (RMBL), in Gunnison County, Colorado. Ponds were selected to span the range of pond sizes present in the upper East River drainage basin, and to include both naturally fishless ponds and those containing brook trout (*Salvelinus fontinalis*). Fish and fishless ponds occurred throughout the drainage basin, often in close proximity (hundreds of meters; Caudill 2002).

Trout densities

Brook trout were the only species of fish observed in the ponds during 1997–2000. Fishless ponds were not predator free and had higher densities of non-fish predators (dytiscid beetles and salamanders) than ponds with trout (Caudill 2002), which may have reduced differences in mayfly adult production and population growth rate observed between fish and fishless ponds. Trout population size was estimated by electroshocking using a three-pass depletion method (Carle and Strube 1978, Cowx 1983). Fishless ponds were also shocked to confirm their fishless status, and as a sham control. Trout densities (number of trout/100 m²) were estimated using the maximum weighted likelihood algorithm of Carle and Strube (1978) and estimates of pond area. Trout densities among ponds and between years were considered significantly different if 95% confidence intervals between estimates did not overlap.

Four treatments (trout control, fishless control, trout reduction, and trout introduction) were assigned to three ponds each, for a total of 12 ponds. Trout densities were manipulated at the end of the *Callibaetis* recruitment period in September 1998. In trout control ponds, fish were immediately returned to the pond. Trout from trout reduction ponds were released into trout introduction ponds. Trout introduction ponds were separated from other naturally fishless ponds by dispersal barriers. Quantitative depletion sampling by electroshocking at two trout control ponds (Marmot and Texas Fishing Bridge) could not be conducted safely. Thus densities reported are minimum estimates based on the number of trout captured. Depletion electroshocking was also ineffective in estimating population sizes and removing fish from introduction ponds at the end of the experiment in 1999 (the ponds were too deep). Partial removal and quantification of trout populations were undertaken in 1999 using electroshocking and short-term (<4 h) gillnet sets. Complete removal of trout from introduction ponds was accomplished in June 2000 using further gill net sets and electroshocking in partially drained ponds (for further details see Caudill 2002). The minimum trout density in introduction ponds at the end of the experiment was calculated as the numbers removed in late 1999 and June 2000, which underestimates the actual trout density during development of the 1998–1999 *Callibaetis* cohort because it does not account for mortality during the winter of 1999–2000.

Habitat characterization

Several physical habitat features were measured in 1998 to test whether the distribution of trout covaried with habitat features that might influence *Callibaetis* fitness. Elevation of each pond was determined from USGS 1:25 000 topographic maps. Pond size and the extent of four microhabitat types within each pond (bare substrate, organic detritus, submerged macrophytes, and *Carex* spp. emergent sedges) were estimated using a surveying autolevel. Mean and maximum water depth were estimated from 42 to 78 points at 1–2-m intervals along four to six randomly placed transects at each pond. At each pond, temperature in the sedge habitat was recorded every 15 min from 26 June to 10 August 1998 using Tidbit digital temperature recorders (Onset Corporation, Bourne, Massachusetts, USA). Principle components analysis (PCA) summarized variation in these 11 habitat variables, and multiple binary logistic regression was used to test whether the distribution of trout (presence or absence) prior to the manipulation of trout densities could be predicted from the PCA component axes (Hosmer and Lemeshow 1989). Components were rotated using the VARIMAX algorithm and gamma = 1.0.

Callibaetis larvae consume detritus, decaying plant material, and associated microcommunities (Edmunds et al. 1976, Berner and Pescador 1988, Da Silva 1997;

personal observation). As a preliminary measure of food availability, percent benthic organic matter (BOM) was estimated in 1999 using duplicate 4×8 cm benthic cores taken from the sedge microhabitat in association with larval samples. Cores were dried at 60°C to constant mass, homogenized, and a subsample was weighed and ashed at 500°C to constant mass to determine percent BOM.

Callibaetis recruitment, emergence rate, adult survival, and λ_i

The life history of *Callibaetis* facilitated the estimation of λ_i for each pond i because recruitment could be estimated during the oviposition and larval stages, all growth occurs during the larval stages, the last larval instar was easily recognized, and because size at emergence is a strong predictor of fecundity in females (Caudill and Peckarsky 2003). At RMBL, larvae grow and develop in ponds from July–September until the next summer. Just prior to emergence, last instar larvae are easily distinguished by the presence of black wing pads (BWP stage). Adults emerge from ponds mid-June through August, and mate. Females return to ponds two weeks later where they lay a single clutch of fully developed eggs, often in a non-natal pond, and subsequently die on the surface of ponds as “spent females” (see Plate 1). *Callibaetis* eggs hatch immediately and larvae initiate feeding within hours (Appendix A; Caudill 2002).

Callibaetis fitness components were partitioned into survival of the nonfeeding adult stage, s_a , survival during larval development in pond i , s_i , and mean fecundity of females for pond i , f_i :

$$\lambda_i = s_i \times s_a \times f_i$$

where

$$s_i = (n_a)_i / (n_r)_i$$

and $(n_a)_i$ was the number of emerging females from pond i and $(n_r)_i$ was the number of female recruits estimated from larvae, $(n_l)_i$ and as eggs from spent females, $(n_e)_i$. All calculations were performed for females by assuming a 1:1 sex ratio and dividing abundances by two. The $(n_a)_i$ were estimated using benthic density estimates and estimates of microhabitat area in each pond as follows. BWP larvae were sampled on eight to 10 dates throughout the 1999 emergence season (3 June–31 August) from the dominant three microhabitats in each pond (typically bare substrate, aquatic macrophyte beds, and emergent sedge beds). On each sample date the density of BWP larvae was determined from a 0.145-m^2 sample collected with a drop column and 25 scoops of a D-net (1-mm mesh). Larvae were live-picked in the field because they are very active and conspicuous swimmers, and were preserved in ethanol. Annual emergence rates of females for each microhabitat were estimated by integrating under curves of BWP density across eight to 10 sampling dates as

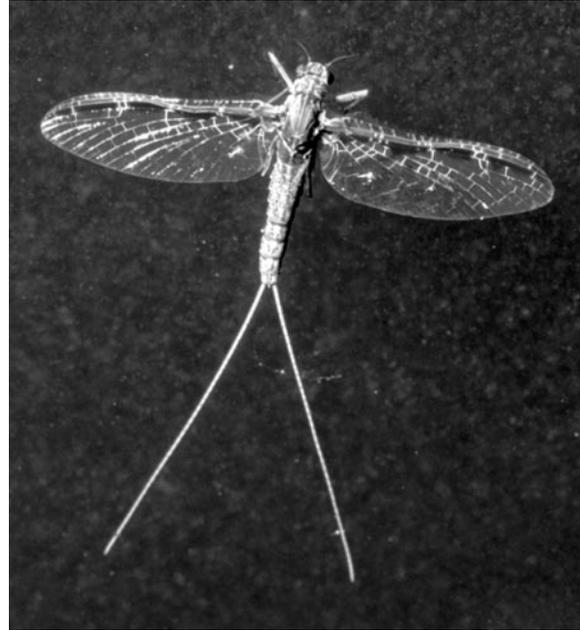


PLATE 1. Female *Callibaetis ferrugineus hageni* imago (the second of two winged stages in mayflies) on the surface of a beaver pond. These “spent females” die after oviposition and were used to estimate larval recruitment to each pond. Photo by Angus McIntosh.

in Peckarsky et al. (2000), and dividing by 5, assuming a five-day BWP period. Finally, annual pond-wide emergence rates for adult females, $(n_a)_i$ were estimated for each pond i by multiplying microhabitat-specific emergence rates by the area of each microhabitat within pond. Using BWP larvae to estimate adult emergence probably overestimated emergence, and λ_i , from ponds with trout due to predation during emergence.

Pond-wide recruitment of larvae, $(n_l)_i$, was estimated using a similar approach. Recruitment for the 1998–1999 cohort was based on samples collected from each microhabitat on the final two dates of 1998 field season (1–22 September) after the oviposition season. Mean densities within each habitat were multiplied by habitat areas to estimate pond wide population sizes of recruits. *Callibaetis* spp. are ovoviviparous (Berner and Pescador 1988), *C. f. hageni* larvae initiate feeding within minutes of oviposition (*personal observation*), and hence egg survival was assumed to be 1.0. Larval recruits were sampled as stage I and II (of VII, Caudill 2002), where stage I larvae are newly hatched, and therefore the sampling method may not have accounted for some early instar mortality. Consequently, reported λ_i may slightly overestimate the true λ_i , though this stage was short (days) compared to the rest of the larval period (9–11 months). Regardless, any unaccounted variance in early instar mortality among ponds should act to decrease differences in estimated λ_i among ponds, thereby obscuring patterns rather than creating false differences between pond types.

I also estimated the annual number of female eggs deposited per pond, $(n_{re})_i$ to compare λ_i using both recruitment estimates. Egg recruitment was estimated as $(n_{of})_i \times f$, where f was the weighted mean fecundity of BWP larvae emerging from all ponds and $(n_{of})_i$, the number of ovipositing females, was estimated by collecting all spent females from the 1997–1998 cohort from the entire surface of each pond on six to eight dates during the oviposition period in 1998, and integrating under curves of oviposition rate versus time (Caudill 2003a). Larval recruitment estimates were used in most calculations because the methods used to estimate larval recruitment were more similar to those used to estimate adult emergence than those used to estimate egg recruitment.

Survivorship of adults emerging from the 1997–1998 cohort in the common terrestrial environment, s_a , was assumed to be constant regardless of natal pond and was estimated as $\Sigma (n_{oi})_i / \Sigma (n_{ao})_i$, where $(n_{ao})_i$ was the number of emerging females in the 1997–1998 cohort. This estimate of s_a includes mortality during the larval BWP stage before emergence to the terrestrial stage. Since mortality in these stages was probably higher in trout ponds, and this mortality was absorbed by the constant s_a term, higher BWP mortality in trout ponds may have produced underestimates of λ_i in fishless ponds. Estimates of $(n_{ao})_i$ for the 1997–1998 cohort were obtained using identical methods as used for the 1998–1999 cohort (Caudill 2003a).

Size and fecundity are related in several mayfly taxa (Peckarsky et al. 1993 and references therein), including *C. f. hageni*, because females are semelparous and do not feed as adults (Edmunds et al. 1976). The mean fecundity of females emerging from each pond was estimated using the mean size of BWP head capsule width (h_{cw}, in mm) of females and the regression equation $f_i = 1580.3 \times \text{h_{cw}} - 1667.7$ ($P < 0.001$, adjusted $r^2 = 0.965$, $n = 7$; Caudill and Peckarsky 2003). Only females emerging from sedge microhabitat were included in the analysis because 83.8% of all individuals emerged from this habitat, and differences in size at emergence among ponds were much greater than among microhabitats within pond (size at emergence data are given in Caudill and Peckarsky 2003). Size at emergence was averaged from larvae emerging from two years (1998 and 1999) for each pond because female size did not differ between years (Caudill 2002, Caudill and Peckarsky 2003). Sample sizes at each pond ranged from 3–143 females, due to differences in larval abundance at each pond. Dissections included females spanning the entire range of BWP larval size observed in the 1998–1999 cohort.

Data analysis and Monte Carlo simulations

A goodness-of-fit test was used to test whether the larval survivorship in individual ponds differed significantly from the average larval survivorship of the metapopulation using expected frequencies based on a

hypothesis intrinsic to the data and a William's correction to estimate χ^2 (G test; Sokal and Rohlf 1995). Survivorships were compared indirectly by testing whether the observed emergence differed significantly from expected emergence given the observed recruitment, the mean metapopulation larval survival rate, s , and weighted mean female fecundity, f . The expected emergence frequency, $E(n_a)_i$, was calculated as:

$$E(n_a)_i = (n_i)_i \times s$$

where

$$s = \frac{\sum (n_a)_i}{\sum (n_{ri})_i}$$

I used Monte Carlo bootstrap simulations to examine whether ponds differed from the equilibrium population growth rate ($\lambda = 1.0$) and to determine whether λ_i differed among ponds. I conducted simulations under model scenarios differing in assumptions about recruitment because the sampling protocol did not provide straightforward estimates of precision for recruitment within each pond. Model 1 used the point estimates of larval recruitment $(n_{ri})_i$, Model 2 used the point estimates of egg recruitment $(n_{re})_i$, and Model 3 randomly varied recruitment about the observed $(n_{re})_i$ value. In each scenario, a bootstrap analysis was performed for each pond to generate a 95% CI about λ_i by randomly varying emergence and/or recruitment and calculating λ_i using a fixed f_i and the point estimate of s_a values for each iteration.

I used a jackknife procedure to estimate standard errors for each $(n_a)_i$. Recall the annual pond-wide population size of emerging adults at each pond represented a point estimate based on the integration of density estimated in three habitats at each pond over multiple dates through the emergence season. At each pond, the jackknife procedure (Dixon 1993) calculated a pseudo-value for emergence, p_k , for $(n_a)_i$ using all observation except those on the first sampling date, $k = 1$. This process was sequentially repeated for the remaining $k - 1$ sampling dates, and a standard error estimated from the distribution of the $\log_e(p_k + 1)$. The p_k were \log_e transformed to prevent negative emergence and survival values in the bootstrap analyses. In each bootstrap iteration, j , $(n_a)_j$ was generated as $\log_e(n_a)_j = \log_e(n_a + 1)_i \pm e_{ij}$, where e_{ij} was a random variate drawn with replacement from a normal distribution with mean of zero and a standard deviation, S_i , equal to 1 SE of mean emergence at pond i , and $(n_a)_j = [\exp(\log_e(n_a)_j - S_i^2/2)] - 1$.

The effect of uncertainty in recruitment was assessed by comparing Model 1 and 2 simulations, which used the two estimates of recruitment, $(n_{ri})_i$ and $(n_{re})_i$. For Model 3, I used linear regression to predict $\log_e((n_{ri})_i)$ from $\log_e((n_{re})_i)$ to obtain a standard error for each $\log_e((n_{re})_i)$. The simulations used the standard error from the confidence interval of the expected value of

y given x in linear regression (Zar 1999:339). The point values of $(n_{re})_i$ and associated standard deviation were used to generate $(n_{tj})_i$ in simulations using the same methods used to generate $(n_{aj})_i$ at each pond. Iterations were performed 5000 times for each pond and fecundity scenario. Methods used in the simulations, including calculation of percentile confidence intervals, were those outlined in Dixon (1993). If the 95% CI did not include 1.0 under all three fecundity scenarios, λ_i was considered significantly different from 1.0. Simulations were programmed and run in Matlab version 7.0 (Mathworks, Inc., Natick, Massachusetts, USA).

Within each recruitment scenario, I also conducted simulations under three assumptions of fecundity (mean, low, and high) for a total of nine simulation scenarios. The value of f_i was determined for the mean fecundity scenario using the mean hcw of larvae from each pond and the relationship between hcw and fecundity. The 95% CI for mean fecundity was calculated incorporating uncertainty in both mean hcw at each pond and the hcw-length regression by first estimating the 95% CI for mean hcw. The lower limit of fecundity was estimated by calculating the lower limit of the 95% CI for the expected value of mean fecundity using the hcw-fecundity equation and the lower 95% CI limit of mean hcw as the predictor (Zar 1999:339). The upper fecundity limit was estimated in a similar fashion using the upper limit of mean hcw.

Adult survival, s_a , has a strong effect on λ_i in *Callibaetis* (Caudill 2003a). Changes in s_a alter the magnitude of λ_i at all ponds simultaneously, and would have little effect on the difference in λ_i among ponds or pond types. Hence, I chose to examine the influence of variation in s_a qualitatively as in Caudill (2003a) by calculating λ_i over a range of assumed s_a values. I used bootstrap simulations to estimate the precision of s_a . In each of 5000 iterations, an $(s_a)_j$ was calculated by resampling and summing the point estimates of $(n_{oi})_i$ and $(n_{ao})_i$ with replacement 12 times. A 95% CI for s_a was calculated from this sampling distribution as above.

The trout manipulation was designed to test experimentally the effect of trout on λ_i . While the manipulation achieved target trout densities in the reduction and introduction treatments, natural variation within the trout control treatment resulted in greater variability within this treatment than among treatments (see *Results: Trout densities*), rendering a traditional ANOVA analysis inappropriate. Hence, I used linear contrasts to test for differences in the point estimates of λ_i between fishless control and introduction treatments, and between introduction and reduction treatments (the variability within the trout control treatment resulted in similar trout densities within trout control vs. reduction treatments, and this contrast was not performed). To maximize statistical power, I also tested for a difference between fishless control ponds and all trout ponds. In addition, I used multiple regression models to describe the relationships of adult emergence for the 1997–1998

cohort and λ_i in the 1998–1999 cohort with trout density and other habitat descriptor variables. The multiple regression of 1997–1998 emergence rates included trout density and three PCA scores for each pond used to predict the distribution of trout. The multiple regression for λ_i used a similar model with the inclusion of percent benthic organic matter (BOM) as a potential measure of resource availability and the number of recruits/m² to the 1998–1999 generation in each pond to test for potential effects of intraspecific competition. PCA scores could not be calculated for 25% of the ponds for the 1998–1999 cohort because of temperature loggers lost during winter 1998–1999. Hence, PCA scores were recalculated using the remaining eight habitat variables. There was no evidence of a temperature effect on adult emergence rate in the 1997–1998 cohort or λ_i in preliminary analyses (Caudill 2002). Regression models were estimated in Systat, version 10 (Systat Software, Inc. Point Richmond, California, USA), using automatic backward stepwise regression (Zar 1999) with $\alpha = 0.15$ for predictor removal.

RESULTS

Trout densities

No trout were found in fishless ponds during the study. Trout densities in the trout reduction ponds were reduced by a factor of 3.61 to 24.4 between 1998 and 1999 (Fig. 1), though not all trout were removed from the reduction ponds. Densities in introduction ponds were similar to each other and to natural levels in trout controls at the time of introduction, declined during the experiment, and remained above the reduction pond trout densities (Fig. 1). Notably, the densities in unmanipulated trout control ponds declined significantly from before to after the manipulation (Fig. 1).

Habitat characterization

The PCA analysis of 11 habitat variables measured in 1998 (Appendix B) revealed three components that explained 79.6% of the total variance among ponds. These components were strongly influenced by temperature, pond and habitat area, and depth, respectively (Caudill 2002). Plots of component scores revealed that pond types (fish and fishless) overlapped in habitat characteristics (Appendix C). The distribution of trout prior to the trout manipulation could not be predicted statistically from the 1998 component scores (multiple logistic regression, $n = 12$, model $P = 0.138$), suggesting that fish and fishless ponds did not differ in estimated habitat parameters and that other factors, such as dispersal barriers, control the distribution of trout among ponds.

Callibaetis recruitment, emergence rate, adult survival, and λ_i

Larval and egg estimates of recruitment agreed at most ponds, though egg recruitment markedly over-

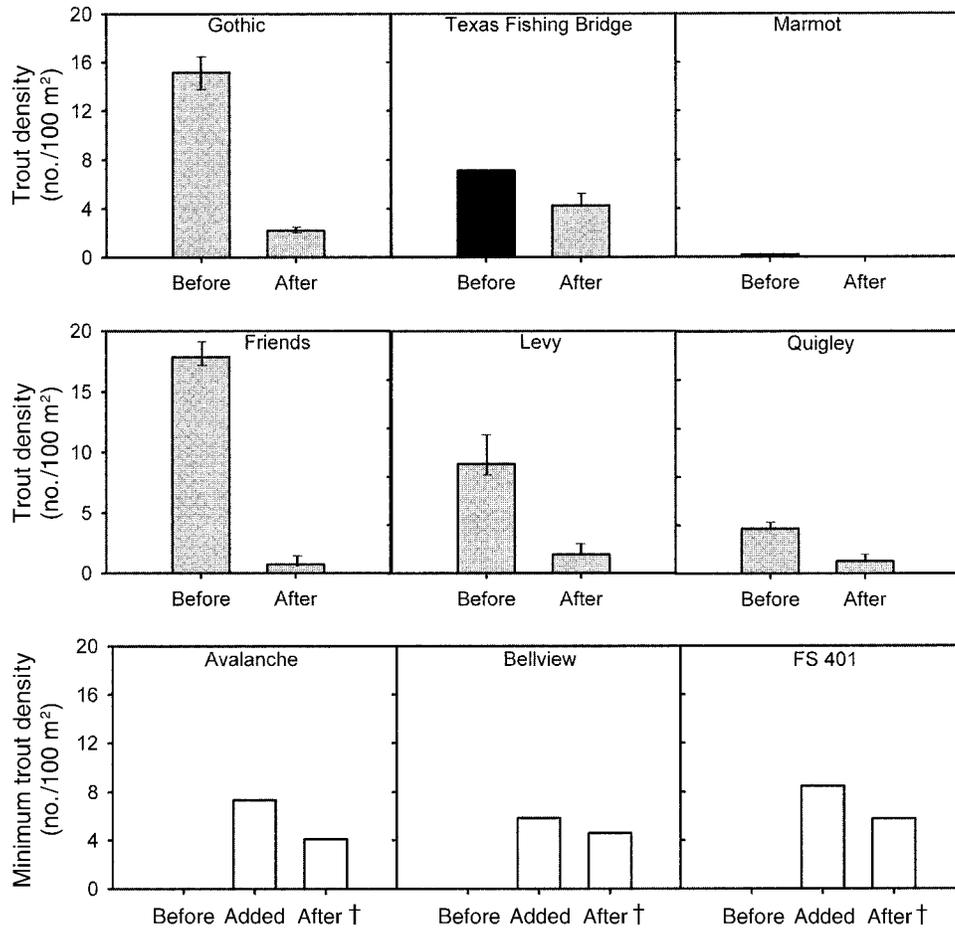


FIG. 1. Trout density before and after the manipulation. The top three panels show trout control ponds; the middle three panels show trout reduction ponds; the bottom three panels are introduction ponds. Three fishless control ponds had no trout before or after the manipulation of trout (not shown). Open bars represent densities released into introduction ponds. Black bars denote sampling periods where quantitative estimates were not feasible and represent minimum density estimates. Similarly, the "after" densities in the introduction ponds represent minimum estimates (indicated by daggers [†]). Error bars are 95% confidence intervals.

estimated larval recruitment at the ponds Marmot and Bellview, and underestimated recruitment at Levy ($\log_e(n_{re})_i = 0.900 \times \log_e(n_a)_i + 1.496$, $n = 12$, $P = 0.016$, $R^2 = 0.458$; Appendix D). Larval recruitment density (larvae/m²) was less variable than adult emergence rates among ponds (Caudill 2003a). Consequently, larval survivorship differed by an order of magnitude among ponds and survivorship among ponds differed significantly from the average survivorship of larvae in the metapopulation (Table 1, G test, $P < 0.001$). In contrast, mean fecundity among ponds differed by a factor of 1.92 or less and λ_i was more sensitive to changes in larval survival than in fecundity (Appendix E).

Point estimates of λ_i varied from 0.062–2.631 (Table 1). All nine Monte Carlo simulation scenarios incorporating estimation error in emergence and fecundity revealed that *Callibaetis* λ_i at four ponds were sinks, with λ_i significantly lower than the equilibrium rate (λ_i

significantly lower than the equilibrium rate $\lambda_i = 1.0$, Appendix F). At four ponds (Avery, Bellview, UBBP, and Marmot) λ_i was significantly greater than replacement (sources) under some, but not all, assumptions of recruitment and fecundity. There was at least one source pond present in the metapopulation under all scenarios, however the identity of this pond changed across scenarios (Appendix F). Comparison of Model 1 and 2 λ_i calculated using larval and egg recruitment produced similar results at 10 ponds. At Bellview and Marmot, the Model 2 and 3 estimates of λ_i were probably unrealistically high, perhaps because lower than expected egg recruitment at these ponds (Appendix D) inflated larval survival.

Adult female survival, s_a , in the larger regional terrestrial habitat was approximately six times lower than average larval survival in ponds (1.67% vs. 9.90%, Table 1). Notably, variation in adult survivorship had the potential to alter the status of ponds as sources or

TABLE 1. Trout density, pond-wide population sizes of recruits and emerging adults, and demographic parameter estimates, λ_i , and the lowest and highest λ_i from nine Monte Carlo simulation scenarios estimating 95% CI of λ_i under different emergence, recruitment, and fecundity assumptions.

Pond (treatment)	Trout density (no./100 m ²)		No. recruits/ pond (n_r) _{<i>i</i>}	No. emerging/ pond (n_a) _{<i>i</i>}	Larval survival (s_i)	Mean fecun- dity (f_i)	95% CL	λ_i	Lowest λ_i	Highest λ_i
	1998	1999								
Avery (NFC)	0	0	2 146 229	332 238	0.1548	1020	930, 114	2.631	0.680	9.660
Rustlers (NFC)	0	0	1 171 234	60 949	0.0520	835	746, 926	0.724	0.146	2.180
UBBP (NFC)	0	0	831 620	121 487	0.1461	739	660, 816	1.799	0.620	3.530
Marmot (TC)	(0.175)	0.09	13 062 969	1 398 789	0.1071	947	854, 1045	1.689	0.679	30.700
Friends (T-)	17.9	0.73	547 325	49 488	0.0904	929	843, 1019	1.399	0.273	4.210
Quigley (T-)	3.72	1.03	483 023	3368	0.0070	531	400, 650	0.062	0.007	0.331
Levy (T-)	6.7	1.58	27 881	179	0.0064	823	594, 1054	0.088	0.000	0.684
Gothic (TC)	15.2	2.2	417 620	7618	0.0182	797	253, 1337	0.242	0.020	4.230
Avalanche (T+)	0	4.1	295 397	2582	0.0087	831	733, 929	0.121	0.030	0.323
TxFsBr (TC)	(7.12)	4.24	644 131	9642	0.0150	822	678, 967	0.205	0.041	0.876
Bellview (T+)	0	4.53	1 399 742	188 070	0.1344	886	802, 972	1.983	0.624	134.000
FS 401 (T+)	0	5.75	1 212 926	26 274	0.0217	971	874, 1073	0.350	0.015	1.460
Metapopulation			22 240 097	2 200 684	0.09895	936	806, 952	1.544		

Notes: Adult female survivorship was calculated for the regional metapopulation, and all local population growth rate estimates were calculated using an adult survival rate of 1.667% (see *Methods* for further details). Treatment codes correspond to no-fish control (NFC), trout control (TC), trout addition (T+), and trout reduction (T-). Ponds are listed in order of increasing 1999 trout density. Trout densities at two ponds represent minimum estimates and are given parenthetically. Metapopulation fecundity is estimated from the mean size of larvae per pond, weighted by the number emerging. Bold type denotes ponds with λ_i significantly different than the equilibrium growth rate (1.0) under all nine simulation scenarios.

sinks in this metapopulation (Caudill 2003a). Calculation of λ_i across the estimated 95% CI of s_a generated in the bootstrap analysis (0.0073–0.0485) revealed two ponds were sinks across all recruitment and fecundity scenarios (Avalanche $\lambda \leq 0.940$; Quigley $\lambda \leq 0.963$). Similar to the simulation results, the presence of a source pond was less certain when s_a was varied. For instance, a decrease in s_a by 28% to 0.012 resulted in the 95% CI of all λ_i including 1.0 under the larval recruitment, mean fecundity scenario.

Among ponds, λ_i and adult mayfly emergence rate from sedges were negatively and nonlinearly related to trout density (Fig. 2, Tables 2 and 3). However, the contrasts among treatments testing for an effect of trout on λ_i provided no evidence that the manipulation of trout density affected λ_i (all contrast $P \geq 0.119$; Appendix G). The lack of response may have resulted from natural variation in λ_i among ponds within treatment, the low statistical power of the design, the short period of manipulation (approximately one mayfly generation), and/or alternative factors. Nonetheless, the negative, nonlinear relationship between emergence rate and trout density in 1998 and 1999, and λ_i and trout density in 1999 (Fig. 2) suggested constrained variance in *Callibaetis* λ_i at higher trout densities where ponds with trout densities <1 trout/100 m² were sources or sinks and ponds with trout densities >~1 trout/100 m² were sinks (Fig. 2). The overall regression model relating λ_i to trout density and environmental variables was marginally significant ($P = 0.069$, Table 3a) when all ponds were included. One introduction pond, Bellview, was an exception to this pattern, having a high point estimate of sedge emergence rate and λ_i in 1999. At least two factors may have contributed to this ob-

servation. First, Bellview had a high *Callibaetis* density and the second highest sedge emergence rate prior to the trout manipulation (Caudill 2002). Hence, per capita *Callibaetis* mortality due to trout may have been low, despite high rates of consumption by trout. Second, trout may have switched to alternative prey because Bellview had an unusually rich and large-bodied invertebrate community structure, including high densities of *Gammarus* amphipods, a hypothesis supported by qualitative analysis of trout guts (Caudill 2002). Removal of the pond Bellview from the regression model produced a highly significant model and a two-fold increase in model R^2 (Table 3b). Neither emergence rate nor λ_i were related to other habitat predictors (Tables 2 and 3), though the effect of area was marginally significant in the reduced λ_i model (Table 3b). While the results of the multiple regression analyses were consistent with the hypothesis that trout affect *Callibaetis*, the lack of a significant treatment effect suggests the potential that alternative mechanisms such as unmeasured habitat covariates affecting both trout and *Callibaetis* were responsible for the negative relationship between trout density and *Callibaetis* λ_i . Nonetheless, on average, habitats that supported high densities of trout were poor habitats for *Callibaetis* larval development.

DISCUSSION

Vital rates indicated both source and sink patches in the metapopulation, and high trout densities were associated with low *Callibaetis* λ_i such that mayfly populations in ponds with high trout density would presumably go extinct in the absence of immigration from sources. For example, population projections assuming

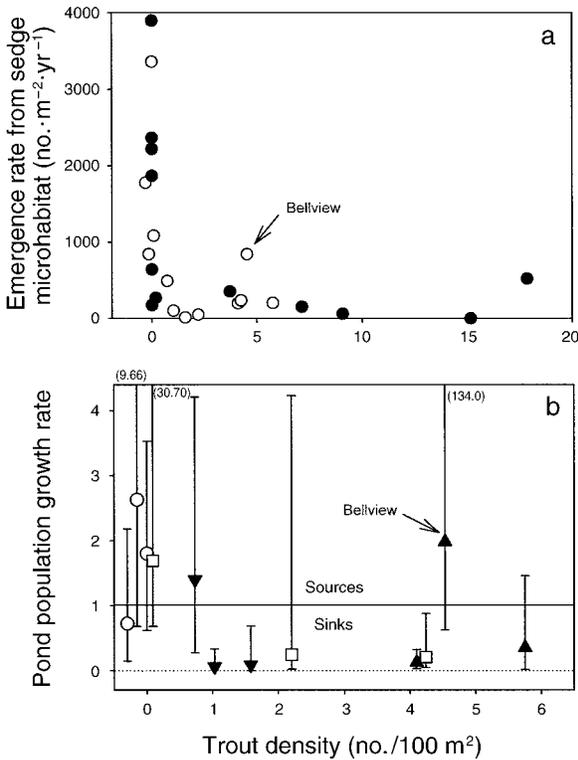


FIG. 2. (a) Emergence rate from the sedge microhabitat before and after the manipulation: solid circles, 1998; open circles, 1999. (b) Relationship between trout density and λ_i after the trout manipulation: open circles, fishless control; open squares, trout control; solid triangles (point up), trout introduction ponds; solid triangles (point down), trout reduction ponds. Note the change in the range of trout density between the plots, which reflects an overall reduction of trout density from 1998 to 1999. Data for fishless controls in panel (b) are slightly offset for clarity. Error bars represent the highest and lowest λ_i from nine Monte Carlo simulation scenarios (Appendix F); the upper confidence limit is given parenthetically for three ponds.

closed populations, constant conditions, and initial population sizes equal to point estimates of recruitment for ponds with λ_i significantly below replacement suggest extinction at these locations in five to nine generations, despite initial population sizes of more than a quarter million. Temporal variation in vital rates can affect the status of subpopulations as sources or sinks (Johnson 2004), and whether demographic rates within

ponds and adult survival in the terrestrial environment remain constant through time is difficult to assess given the short-term nature of this study. Adult emergence rates from the 1997–1998 cohort suggest that the metapopulation as a whole imported individuals (a putative sink, Caudill 2003a). In contrast, the 1998–1999 cohort estimate of λ for the metapopulation indicated the metapopulation acted as a net source. To what degree this interannual variation represents sampling error versus natural variation remains unknown. At the local scale, patterns of larval abundance among ponds over three generations, and emergence and oviposition over two generations suggest a more stable pattern and that larval *Callibaetis* survival is generally higher in fishless ponds (Caudill 2003a, this study). Clearly, estimates of demographic rates over several generations are needed to determine whether subpopulations in identified sinks would decline to extinction in the absence of immigration. This is particularly true for those ponds with trout, given the large interannual variability observed in trout density in the trout control ponds.

The results of the simulations supported the conclusion that there were sink patches in the population because λ_i at some ponds remained below replacement under all simulation scenarios and assuming more than threefold increase over the point estimate of adult survival. While λ_i point estimates calculated under all recruitment and fecundity scenarios suggested the presence of 4–5 source ponds and all simulations suggested at least one source, no single pond was a source under all simulation scenarios (Appendix F). Whether this discrepancy resulted from sampling error or the introduction of an unrealistic amount of variability to the simulations is unknown, and it was possible that all ponds were actually sinks. However, the metapopulation λ was greater than 1.0, and remained so for s_a values as low as 65% of the point estimate, suggesting the presence of at least one source subpopulation. The conclusion that at least some ponds represented sources or sinks was generally consistent with an analysis of the 1997–1998 *Callibaetis* cohort (Caudill 2003a). In that analysis, some ponds were importers or exporters of individuals across a large range of assumed s_a values (0.01–0.10). Regardless of the status of individual ponds as sources or sinks, it is unlikely that estimation error generated the pattern observed between λ_i and trout density.

TABLE 2. Final model, backward multiple regression analysis testing for relationships between the \log_e of 1998 adult *Callibaetis* emergence rate, trout density, and three PCA axes primarily describing variation among ponds in temperature, area, and depth.

Source	SS	df	MS	F	Coefficient	1 SE	t	P	Adj. R ²
Regression	5.663	2	2.832	6.696				0.017	0.509
Error	3.806	9	0.423						
Constant					2.988	0.257	11.615	<0.001	
(Trout density) ^{-1/3}					-0.684	0.188	-2.545	0.031	
PCA3 (depth)					0.348	0.207	1.683	0.127	

TABLE 3. Final model, backward multiple regression analysis testing for relationships between the \log_e of 1999 *Callibaetis* λ_i and trout density, *Callibaetis* larval density at recruitment, BOM, and three PCA axes primarily describing variation among ponds in area, depth, and cover.

Source	SS	df	MS	F	Coefficient	1 SE	t	P	Adj. R ²
a) All ponds									
Regression	8.889	2	4.444	3.664				0.069	0.326
Error	10.918	9	1.213						
Constant					0.469	0.573	0.818	0.434	
(Trout density) ^{-1/3}					-1.238	0.498	-2.487	0.035	
PCA3 (cover)					0.563	0.342	1.645	0.134	
b) Excluding Bellview									
Regression	5.925	2	2.963	12.204				0.004	0.691
Error	1.942	8	0.243						
Constant					1.491	0.275	5.424	0.001	
(Trout density) ^{-1/3}					-0.736	0.256	-2.877	0.021	
PCA1 (area)					0.382	0.168	2.273	0.053	

Source-sink metapopulation dynamics in freshwater systems

Despite the intuitive appeal of the source-sink concept, there have been few demonstrations of this dynamic in natural populations (Diffendorfer 1998). The spatial structure inherent to many freshwater habitats, and the life histories and movement behaviors of many taxa that inhabit them, suggest many aquatic taxa exist as metapopulations. In this system, the observed source-sink dynamic appeared to result from frequent movement among ponds by females prior to oviposition (Caudill 2003b), nonselective oviposition by females with respect to trout density (Caudill 2003a), a lack of adaptive behavioral or life history shifts by larvae in the presence of trout (Caudill and Peckarsky 2003), and subsequent low survival in ponds with high trout density (this study). Aquatic taxa with similar traits probably exhibit source-sink dynamics, while those with different dispersal abilities, habitat selection behaviors, and/or behavioral responses to predators will probably exhibit other types of metapopulation dynamics.

Influence of trout on local population growth rate

The experimental manipulation of trout density did not provide conclusive evidence of the anticipated negative effect of trout predation on *Callibaetis* λ_i , perhaps due to the large natural variation in trout density within the trout control treatments, low statistical power, the short-term nature of the manipulation, and the impracticality of precisely manipulating trout densities in the beaver ponds. Nonetheless, the observed relationships between λ_i and trout density and *Callibaetis* emergence rate and trout density during the previous generation were consistent with the hypothesized effect of trout on λ_i and no other putative causal factors (physical habitat descriptors, recruitment density, etc.) were significantly related to the estimates of population growth rate or emergence rate. However, these analyses can not rule out the possibility that the observed patterns were generated by unmeasured, correlated causal fac-

tors and further experimental data are needed to definitively confirm the negative effect of trout on local *Callibaetis* λ .

Assuming the observed pattern between λ_i and trout density reflects the effects of predation by trout, the influence of fish on prey population growth rates is not surprising. Fish have repeatedly been shown to affect lentic macroinvertebrate populations and communities (see Batzer and Wissinger 1996, Wellborn et al. 1996, Batzer et al. 1999 for reviews). Most studies have been in warm water temperate habitats (Hall et al. 1970, Crowder and Cooper 1982, Gilinsky 1984, Diehl 1992, Batzer 1998), and have frequently found little evidence that fish reduce overall macroinvertebrate density or species richness (e.g., Thorp and Bergey 1981, Thorp 1986). Rather, individual taxa respond to the presence or absence of fish predators (e.g., Hall et al. 1970).

Fewer studies are available for lentic cold-water habitats. The available studies provide evidence for a strong trophic interaction between trout and *Callibaetis* mayflies. Luecke (1986, 1990) found that cutthroat trout (*Oncorhynchus clarki*) selectively consumed *Callibaetis* sp. larvae over other invertebrates, selectively consumed larger individuals, and that the introduction of trout was associated with the disappearance of *Callibaetis* sp. from the profundal zone of Lake Lenore, Washington, USA. In a natural experiment, Carlisle and Hawkins (1998) found declines of conspicuous prey taxa in Utah lakes with trout compared to fishless lakes, and diet analyses revealed that cutthroats actively selected *Callibaetis* mayflies in macrophyte microhabitats. In a larger survey, Knapp et al. (2001) found that *Callibaetis* larvae were present in a higher proportion of fishless alpine lakes, and at a much higher density, than lakes that were historically fishless, but had been stocked with native and nonnative salmonids. Several other visually conspicuous and active insect taxa followed the same pattern (e.g., corixids, dytiscid beetles, several genera of caddisflies [Knapp et al. 2001]), suggesting these taxa were vulnerable to predation by visual feeding trout as well. Overall, *Callibaetis* larvae

appear to be highly susceptible to both native and non-native trout.

Notably, several traits of *Callibaetis* suggest it is adapted for a “fast lifestyle” suited to temporary, fishless habitats (Sih 1987). All females in the genus lay fully developed eggs, a trait that reduces larval developmental period (Edmunds 1976, Wiggins et al. 1980, Berner and Pescador 1988). The populations studied here showed no evidence of reduced size at emergence from ponds containing trout (Caudill and Peckarsky 2003), suggesting larvae did not accelerate development to reduce predation risk, as has been observed in stream mayflies (Peckarsky et al. 2001). Additionally, larvae did not reduce size at or time to emergence or reduce their activity when exposed to trout chemical cues in mesocosms (Caudill and Peckarsky 2003). Many other temporary habitat specialists are active and conspicuous (Wiggins et al. 1980), suggesting the potential for source–sink dynamics in these species.

Metapopulation type might often be predicted from prey traits. For example, source–sink dynamics are expected in those taxa with nonselective dispersal and active larvae (Ephemeroptera, *Callibaetis*; Odonata, *Enallagma boreale*, *E. cyathigerum* [McPeck 1989, 1990a, b]; Trichoptera [Wissinger et al. 1999]; Amphibia [Sih et al. 2000]) or taxa that do not recognize and respond to introduced predators (McIntosh and Townsend 1994). Taxa that selectively avoid fish habitats during oviposition (Diptera [Blaustein and Kotler 1993, Angelon and Petranka 2002, Berendonk and Bonsall 2002], Coleoptera [Resetarits 2001], amphibians [Kats and Sih 1992]) or exhibit flexible behaviors or life histories in the presence of fish (Ephemeroptera [Peckarsky et al. 2001], Odonata [Wisenden et al. 1997, Hopper 2001], Coleoptera [Abjörnsson 1997], Gastropoda [Turner and Montgomery 2003]) will probably be best described by other metapopulation dynamics such as the balanced dispersal dynamic (McPeck and Holt 1992). Finally, these results point to the importance of identifying source–sink dynamics in populations of conservation or management concern—effort directed at management targets in sink habitats will have little long-term effect. Notably, this may be especially important in freshwater systems, where fish communities have been strongly altered by intentional introductions of both native and nonnative fishes.

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LITERATURE CITED

- Abjörnsson, K., B. M. A. Wagner, A. Axelsson, R. Bjerselius, and K. H. Olsen. 1997. Responses of *Acilius sulcatus* (Coleoptera: Dytiscidae) to chemical cues from perch (*Perca fluviatilis*). *Oecologia* **111**(2):166–171.
- Angelon, K. A., and J. W. Petranka. 2002. Chemicals of predatory mosquitofish (*Gambusia affinis*) influence selection of oviposition site by *Culex* mosquitoes. *Journal of Chemical Ecology* **28**(4):797–806.
- Batzer, D. P. 1998. Trophic interactions among detritus, benthic midges, and predatory fish in a freshwater marsh. *Ecology* **79**:1688–1698.
- Batzer, D. P., R. B. Rader, and S. A. Wissinger, editors. 1999. *Invertebrates in freshwater wetlands of North America*. John Wiley and Sons, New York, New York, USA.
- Batzer, D. P., and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology* **41**:75–100.
- Berendonk, T. U., and M. B. Bonsall. 2002. The phantom midge and a comparison of metapopulation structures. *Ecology* **83**:116–128.
- Berner, L., and M. Pescador. 1988. *The mayflies of Florida*. Revised edition. Florida A&M University Press, Tallahassee, Florida, USA.
- Blaustein, L., and B. P. Kotler. 1993. Oviposition habitat selection by the mosquito, *Culiseta longiareolata*: effects of conspecifics, food and green toad tadpoles. *Ecological Entomology* **18**:104–108.
- Boughton, D. A. 1999. Empirical evidence for complex source–sink dynamics with alternative states in a butterfly metapopulation. *Ecology* **80**:2727–2739.
- Boughton, D. A. 2000. The dispersal system of a butterfly: a test of source–sink theory suggests the intermediate-scale hypothesis. *American Naturalist* **156**(2):131–144.
- Carle, F., and M. R. Strube. 1978. A new method for estimating population size from removal data. *Biometrics* **34**:621–630.
- Carlisle, D. M., and C. P. Hawkins. 1998. Relationships between invertebrate assemblage structure, 2 trout species, and habitat structure in Utah mountain lakes. *Journal of the North American Benthological Society* **17**(3):286–300.
- Caudill, C. C. 2002. *The metapopulation biology of the mayfly *Callibaetis ferrugineus hageni* in high elevation beaver ponds*. Dissertation. Cornell University, Ithaca, New York, USA.
- Caudill, C. C. 2003a. Empirical evidence for nonselective recruitment and a source–sink dynamic in a mayfly metapopulation. *Ecology* **84**:2119–2132.
- Caudill, C. C. 2003b. Measuring dispersal in a metapopulation using stable isotope enrichment: high rates of sex-biased dispersal between patches in a mayfly metapopulation. *Oikos* **101**:624–630.
- Caudill, C. C., and B. L. Peckarsky. 2003. Lack of appropriate behavioral or developmental responses by mayfly larvae to trout predators. *Ecology* **84**:2133–2144.
- Cowx, I. 1983. Review of the methods for estimating fish population size from survey removal data. *Fisheries Management* **14**(2):67–82.
- Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**:1802–1813.
- Da Silva, E. R. 1997. On the food of nymphs of *Callibaetis guttatus* Navas, 1915 Ephemeroptera, Baetidae) in a temporary marsh at the littoral of Rio De Janeiro State, Brazil. *Revista Brasileira de Entomologia* **41**(1):53–55.

- Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* **73**:1646–1661.
- Diffendorfer, J. 1998. Testing models of source–sink dynamics and balanced dispersal. *Oikos* **81**:417–433.
- Dixon, P. M. 1993. The bootstrap and the jackknife: describing the precision of ecological indices. Pages 290–318 in S. M. Scheiner and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman and Hall, New York, New York, USA.
- Edmunds, G., Jr., S. L. Jensen, and L. Berner. 1976. *The mayflies of North and Central America*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Ferreras, P. 2001. Landscape structure and asymmetrical interpatch connectivity in a metapopulation of the endangered Iberian lynx. *Biological Conservation* **100**(1):125–136.
- Gilinsky, E. 1994. The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology* **65**:455–468.
- Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography* **15**(6):839–928.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27–42 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Hopper, K. R. 2001. Flexible antipredator behavior in a dragonfly species that coexists with different predator types. *Oikos* **93**(3):470–476.
- Hosmer, D. W., and S. Lemeshow. 1989. *Applied logistic regression*. John Wiley and Sons, New York, New York, USA.
- Johnson, D. M. 2004. Source–sink dynamics in a temporally heterogeneous environment. *Ecology* **85**:2037–2045.
- Kats, L., and A. Sih. 1992. Oviposition site selection and avoidance of fish by streamside salamanders (*Ambystoma barbouri*). *Copeia* **1992**:468–473.
- Knapp, R. A., K. R. Matthews, and O. Sarnelle. 2001. Resistance and resilience of alpine lake fauna to fish introductions. *Ecological Monographs* **71**:401–421.
- Luecke, C. 1986. Ontogenetic changes in feeding habits of juvenile cutthroat trout. *Transactions of the American Fisheries Society* **115**:703–710.
- Luecke, C. 1990. Changes in abundance and distribution of benthic macroinvertebrates after introduction of cutthroat trout into a previously fishless lake. *Transactions of the American Fisheries Society* **119**:1010–1021.
- McIntosh, A. R., and C. R. Townsend. 1994. Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. *Ecology* **75**:2078–2090.
- McPeck, M. A. 1989. Differential dispersal tendencies among *Enallagma* damselflies (Odonata) inhabiting different habitats. *Oikos* **56**(2):187–195.
- McPeck, M. A. 1990a. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology* **71**:83–98.
- McPeck, M. A. 1990b. Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. *Ecology* **71**:1714–1726.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* **140**:1010–1027.
- Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* **74**:1836–1846.
- Peckarsky, B. L., B. W. Taylor, and C. C. Caudill. 2000. Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. *Oecologia* **125**:186–200.
- Peckarsky, B. L., B. W. Taylor, A. R. McIntosh, M. A. McPeck, and D. A. Lytle. 2001. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. *Ecology* **82**:740–757.
- Pulliam, H. R. 1988. Sources, sinks and population regulation. *American Naturalist* **132**:652–661.
- Resetarits, W. J., Jr. 2001. Colonization under threat of predation: avoidance of fish by an aquatic beetle, *Tropisternus lateralis* (Coleoptera: Hydrophilidae). *Oecologia* **129**:155–160.
- Sih, A. 1987. Predator and prey lifestyles: an evolutionary and ecological overview. Pages 203–224 in W. C. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Sih, A., L. B. Kats, and E. F. Maurer. 2000. Does phylogenetic inertia explain the evolution of ineffective antipredator behavior in a sunfish–salamander system? *Behavioral Ecology and Sociobiology* **49**(1):48–56.
- Sokal, R., and F. J. Rohlf. 1995. *Biometry*. W. H. Freeman and Co, New York, New York, USA.
- Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London, Series B* **268**:1791–1796.
- Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. *Oikos* **47**:75–82.
- Thorp, J. H., and E. A. Bergey. 1981. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. *Ecology* **62**:365–375.
- Turner, A. M., and S. L. Montgomery. 2003. Spatial and temporal scales of predator avoidance: experiments with fish and snails. *Ecology* **84**:616–622.
- Wellborn, G. A., S. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* **27**:337–363.
- Wiggins, G. B., R. J. Mackay, and I. M. Smith. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. *Archiv für Hydrobiologie Supplement* **58**:97–206.
- Wisenden, B. D., D. P. Chivers, and R. J. F. Smith. 1997. Learned recognition of predation risk by *Enallagma* damselfly larvae (Odonata, Zygoptera) on the basis of chemical cues. *Journal of Chemical Ecology* **23**(1):137–151.
- Wissinger, S., H. H. Whiteman, G. B. Sparks, G. L. Rouse, and W. S. Brown. 1999. Foraging trade-offs along a predator–permanence gradient in subalpine wetlands. *Ecology* **80**:2102–2116.
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice Hall Upper Saddle River, New Jersey, USA.

APPENDIX A

A figure showing the life history of *Callibaetis ferrugineus hageni* and experimental design is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-050-A1.

APPENDIX B

A table showing habitat characteristics of the 12 study ponds is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-050-A2.

APPENDIX C

A figure showing the principle components analysis ordination comparing habitat variables in trout ponds to fishless ponds before the experimental manipulation of trout density is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-050-A3.

APPENDIX D

A figure comparing a regression plot of larval recruitment to recruitment estimated from spent females is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-050-A4.

APPENDIX E

A figure illustrating the relationship between λ_t , larval survivorship, and fecundity is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-050-A5.

APPENDIX F

A table showing the results of nine Monte Carlo simulation scenarios examining the effect of uncertainty in fecundity and recruitment estimates on λ_t is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-050-A6.

APPENDIX G

A table showing the results of linear contrasts testing for differences in λ_t among trout density manipulation treatments is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-050-A7.