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EMPIRICAL EVIDENCE FOR NONSELECTIVE RECRUITMENT AND A SOURCE–SINK DYNAMIC IN A MAYFLY METAPOPULATION

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Abstract. Dispersal among spatially subdivided populations and variability in local habitat patch quality can strongly affect local and regional population dynamics. A metapopulation of mayflies (*Callibaetis ferrugineus hageni*) was studied in which larvae developed in beaver ponds and emerged to the terrestrial habitat as adults; adult females had the potential to disperse among ponds before oviposition. Ponds (patches) differed in the presence or absence of trout. Densities of late instar larvae were more than an order of magnitude greater in fishless ponds.

Estimates of adult production, migration, and oviposition rate were used to determine whether the difference in larval abundance between pond types was more consistent with a source–sink or balanced dispersal model. Patch quality among ponds (estimated by the emergence rate of adults) varied from 0 to ~3900 individuals·m^{-2}·yr^{-1}, and was significantly lower in ponds with trout. Survivorship of adult females in the regional terrestrial habitat was low (1.7%). Consistent with the predictions of source–sink theory, local recruitment to the next generation was not related to local emergence. Moreover, comparison of emergence and recruitment revealed that some ponds were net exporters of females (sources) and others were net importers (sinks). Ovipositing females did not avoid ovipositing in ponds with trout. Overall, the data were consistent with a source–sink dynamic because patches differed in quality, and because there was net migration of individuals from sources to sinks. The results support the hypothesis that local and regional population dynamics are influenced by spatial variation in patch quality, and by the ability of individuals to both disperse among and assess the quality of habitat patches.

Key words: Callibaetis ferrugineus hageni; *dispersal; habitat quality; habitat selection; life histories, complex; mayflies; metapopulation; oviposition; recruitment; source–sink.*

INTRODUCTION

Few populations in nature are truly closed, but rather are regional metapopulations composed of local populations connected by some degree of dispersal (Levins 1969, Hanski and Simberloff 1997, Harrison and Taylor 1997). Recent reviews have identified spatial variation in patch quality and dispersal as major factors influencing local and regional dynamics (e.g., Harrison and Taylor 1997, Thomas and Kunin 1999); and metapopulation models differ considerably in their assumptions about these factors. The suitability or quality of local habitat patches for a species is determined by biotic and abiotic factors, and can be estimated from the local population growth rate in a patch (Kareiva 1990, Dias 1996, Hanski and Simberloff 1997). The pattern of dispersal among patches is determined by the dispersal system of a species, the ability of organisms to disperse among patches, and their behavior in selecting a patch (Boughton 2000).

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In source–sink metapopulations, mortality in sink patches exceeds natality, and sink populations persist due to the net movement of individuals from sources (Shmida and Ellner 1984, Holt 1985, Pulliam 1988; see reviews in Dias 1996 and Pulliam 1996). In source–sink populations, patch selection may be constrained by social interactions (e.g., territoriality; Pulliam 1988), poor dispersal ability (e.g., many plankton), or an inability of dispersing individuals to assess patch quality (nonselective dispersal), forcing some individuals to develop in low quality habitat.

In contrast, in systems with balanced dispersal (McPeek and Holt 1992), dispersal is unconstrained (selective). Mean individual fitness among patches does not differ, because individuals are able to select the patch that will maximize their expected fitness (McPeek and Holt 1992, Lemel et al. 1997). The resulting emigration probabilities are inversely related to patch carrying capacity and per capita immigration to, and emigration from, a patch are equal (i.e., dispersal is ''balanced''; McPeek and Holt 1992). While natural populations are unlikely to fit neatly into the categories proposed by these models (Thomas and Kunin 1999), the categories can be useful heuristically for identifying qualitatively different mechanisms affecting patterns of distribution.

Despite the rich theoretical literature, relatively few empirical studies have assessed the processes explaining observed spatial patterns of abundance and population dynamics (see reviews in Dias 1996, Pulliam 1996, Harrison and Taylor 1997, Diffendorfer 1998). This paucity of examples stems from the practical difficulty of simultaneously collecting vital rates within patches and estimating dispersal among patches in the same population (Harrison and Taylor 1997, Diffendorfer 1998, Thomas and Kunin 1999). Nonetheless, empirical data will become increasingly important as anthropogenic change alters the quality and distribution of habitats. In addition to altered patch quality, an understanding of the processes influencing dispersal is important, because alteration of the landscape matrix where dispersal occurs can affect population and community dynamics (Daily and Erhlich 1996, Boughton 2000, Ricketts 2001).

In this study, patterns of larval abundance, emergence rate to adulthood, recruitment, and oviposition behavior in a metapopulation of the mayfly *Callibaetis ferrugineus hageni* Eaton (Baetidae) were used to distinguish between balanced dispersal and source–sink population dynamic models. Larvae developed in beaver ponds (patches) and winged adults had the potential to disperse among ponds. This life cycle is typical of many insects and amphibians in which adults disperse among relatively discrete larval habitats, and is analogous to that of many plants, parasites, marine invertebrates, and fishes in which a relatively sessile adult produces many small offspring that have the potential for long distance dispersal. The beaver ponds potentially differed in quality based on the presence or absence of predatory trout and variation in other factors affecting larval growth and survival. While observational data alone cannot be used to positively identify underlying mechanisms, models with inappropriate or improbable mechanisms may be tentatively rejected in favor of a model that is more consistent with the data (Hilborn and Mangel 1997, Turchin 1998). Here, production of adults, oviposition rates, and subsequent larval recruitment were estimated to examine (1) whether trout presence reduced adult emergence rate (a surrogate of pond quality); (2) whether females selectively oviposited in ponds of higher quality; and (3) whether net migration from high to low quality ponds occurred. No net migration and selective oviposition would support a balanced dispersal model, while nonselective oviposition and net migration among ponds would support a source–sink model.

Methods

Study system

Callibaetis ferrugineus hageni (hereafter *Callibaetis*) is distributed throughout western North America and is one of the most common mayflies in Colorado (McCafferty et al. 1997). The study system consisted of 12 ponds in separate watersheds in the upper East River valley (Fig. 1) near the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado, USA. In this location, *Callibaetis* larvae are locally abundant in montane beaver ponds, but are rare in other aquatic habitats (Wissinger et al. 1999, Caudill 2002). Larvae develop in the ponds and emerge to the adult stages throughout the summer (Fig. 2). Ponds were sampled during the summers of 1997 and 1998, and samples included all or parts of three generations: end of the 1996–1997, all of the 1997–1998, and the beginning of the 1998–1999 cohorts (Fig. 2). Ponds differed in the presence or absence of predatory brook trout (*Salvelinus fontinalis*), which could influence pond quality for larvae (e.g., Batzer and Wissinger 1996, Wellborn et al. 1996). The presence or absence of trout did not appear to be confounded with variation in 11 habitat variables measured during summer 1998 including pond elevation, temperature, area, depth, and the extent of different microhabitats within ponds (Caudill 2002). Fishless ponds did contain predators, including larval and adult salamanders (*Ambystoma tigrinum nebulosum*) and adult dytiscid beetles (primarily *Agabus tristis* and *A. austinii*, Caudill 2002). Many of the study ponds were part of beaver pond complexes and all ponds were fed by first or second order spring-fed streams. There was little potential for larval dispersal among ponds. *Callibaetis* larvae avoid moving water (Edmunds et al. 1976) and were uncommon along the dam outlets of ponds.

Fish populations

Trout population sizes were estimated by electroshocking using a three-pass depletion method (Carle and Strube 1978, Cowx 1983) at the end of each summer. Presence of fish was established a priori by visual surveys, and presence or absence of trout was confirmed at beginning of each summer by electroshocking. Fishless ponds were electroshocked during each sampling as a sham control. Quantitative sampling at two deep trout ponds (Marmot, Texas Fishing Bridge [TxFsBr]) could not be conducted safely with this method. Consequently, analyses involving fish were restricted to fish presence or absence. All fish were measured (fork length) and released. Fish densities were estimated using the maximum weighted likelihood algorithm of Carle and Strube (1978).

Collection of larval samples

Mayfly larvae were quantitatively sampled with a drop column (0.145 m^2) to estimate abundance, emergence rates, and recruitment. Larvae were removed from the drop column with 25 scoops of a D-net (1-mm mesh) and were separated from organic detritus in pond water in 40 $\times$ 50 cm white trays. *Callibaetis* larvae are conspicuous and active swimmers and samples were examined until more than two minutes had

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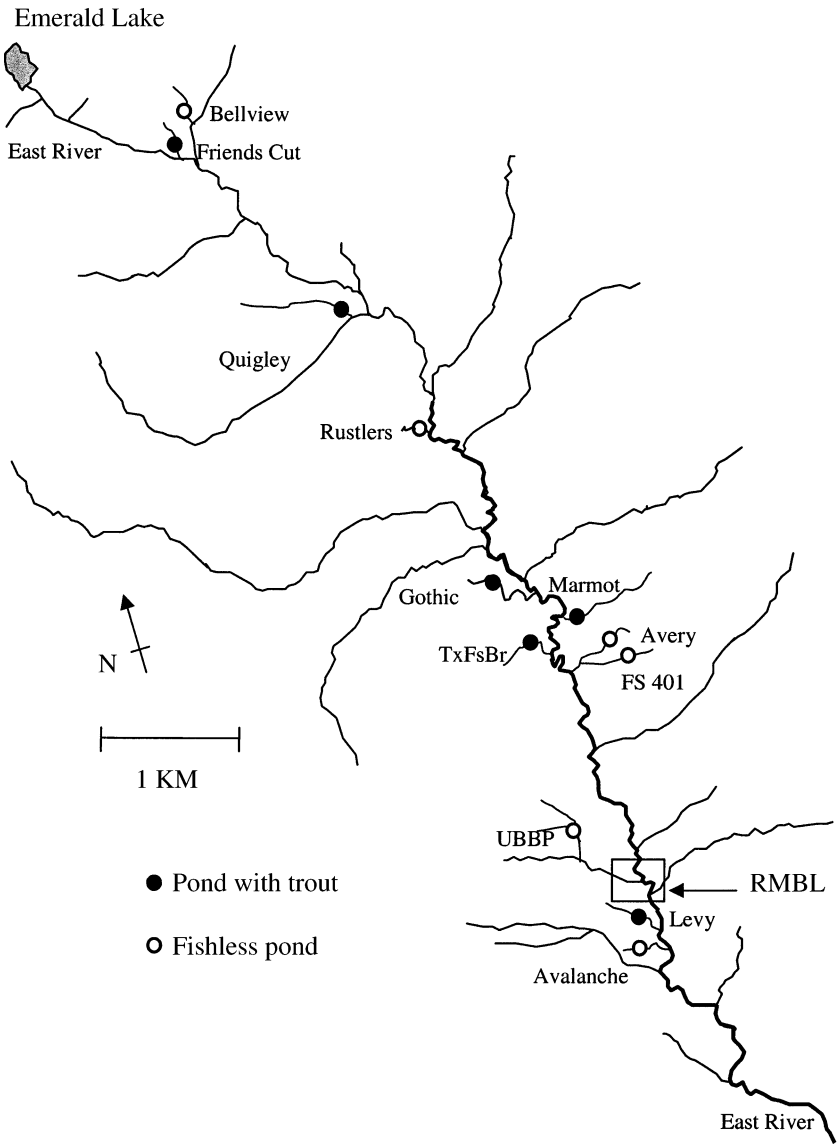


FIG. 1. Map of study sites near the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado (elevation ~2900 m). The Avery and Marmot ponds were added in 1998.

elapsed since the last larva had been removed. Larvae were preserved and stored in 80% ethanol.

Cohorts were distinguished by analyzing stage structure (Caudill 2002). Developmental stages were based on wing pad morphology using criteria modified from Clifford et al. (1979) and Delucchi and Peckarsky (1989) because the number of instars in larvae is indeterminate. Last instar larvae were distinguished by the presence of darkened (black) wing pads (BWP). Stage structure of large samples (>75 larvae) was estimated from subsamples taken by haphazardly distributing larvae in a gridded tray and staging all larvae present in randomly selected grids (minimum = 40 larvae, mean = 64.9), with the exception that all BWP larvae were counted from the entire sample.

Patterns of larval abundance

Larval densities in fish and fishless ponds were estimated near the onset of adult emergence using five samples from each pond. Within each pond, up to four microhabitats were recognized (bare substrate, organic detritus, submerged macrophyte beds, and emergent sedge beds). The five samples from each pond were allocated so that all microhabitats were sampled, and microhabitats with high relative cover were sampled multiple times. Ten ponds were sampled in 1997 (1996–1997 cohort) and 12 ponds in 1998 (1997–1998 cohort; Fig. 2). Habitat structure associated with each larval sample was estimated as the dry mass of plant material in each sample. The submerged portion of plants and coarse detritus were collected from samples after the

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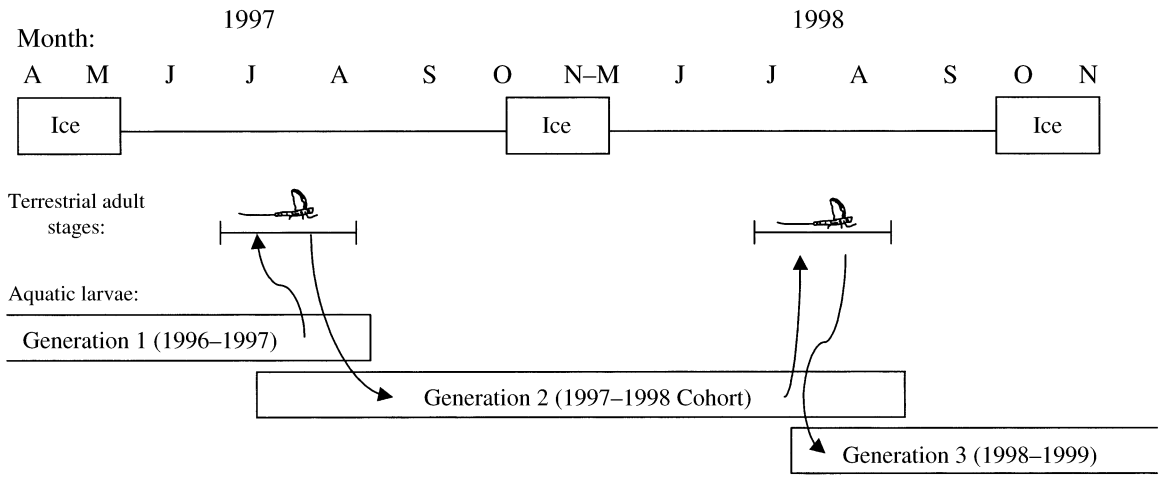


FIG. 2. Life history of *Callibaetis ferrugineus hageni*. Larvae developed in beaver ponds and overwintered in mid to late larval stages. The study population was univoltine, and adults emerged from mid-June through August. Females of this species mate immediately after emerging from the ponds as subimagos (the first, and typically prereproductive, winged stage in mayflies) in swarms of male imagos (the second and terminal winged stage). Female imagos return to the ponds two weeks later, which is unusually long for mayflies, to lay fully developed (ovoviviparous) eggs during the afternoon in a single pond (Caudill 2002). After oviposition, ''spent'' females retain no eggs and can fly no more than a few meters, where they usually die on the water surface (Caudill 2002). Three generations of *Callibaetis* were examined in each pond during the 2-yr study. Larval abundance was estimated for the 1996–1997 and 1997–1998 cohorts just prior to emergence in June. The 1997–1998 cohort was also sampled intensively during emergence. The 1998–1999 cohort was sampled throughout the recruitment period.

invertebrates were removed, sieved over 2-cm wire mesh, and dried at 60°C to constant mass.

Adult emergence and larval recruitment

The emergence rate (adults·m^{-2}·yr^{-1}) was examined as a surrogate of local population growth rate, a measure of habitat quality for larvae (Caudill 2002), and was also compared to subsequent larval recruitment. In summer 1998, repeated larval samples were used to estimate adult emergence rate for the 1997–1998 cohort using densities of BWP larvae. On each of eight to 10 sampling dates between 10 June and 22 September, three samples were taken from each pond in three different microhabitats (typically bare, macrophyte, and sedge). Using BWP larvae to estimate emergence probably overestimated emergence from trout ponds, since mortality during the BWP and subimago stages was probably higher in trout ponds. Trout stomachs frequently contained *Callibaetis* larvae (Caudill 2002), trout prefer larger sized prey (Rader 1997), and trout were frequently observed consuming subimagos at the surface. Thus, reported differences in emergence rate between fish and fishless ponds are probably conservative. The emergence rate from each of the three microhabitats in each pond was estimated by integrating under curves of BWP density over time (as in Peckarsky et al. 2000) and assuming a 5-d BWP period (Caudill 2002). Larval recruitment to the 1998–1999 cohort was estimated using the mean density of larvae (larvae/m^2, all stages) sampled in three microhabitats in each pond and averaged over the last two sampling dates (September).

The relationship between the total (pond-wide) population size of emerging adults and subsequent pond-wide recruitment was also examined because these parameters are correlated in a balanced dispersal dynamic, but not in a source–sink dynamic. The pond-wide population size of emerging adults for each pond was estimated by multiplying habitat specific emergence rates by the area of each microhabitat within each pond. Similarly, recruitment at the pond-wide scale was estimated by multiplying habitat-specific estimates of larval recruit density by habitat areas for each pond.

Oviposition

Female oviposition was examined by collecting spent females from the entire surface of each pond on six to eight dates in 1998. Annual oviposition rate (no. females/yr) was estimated by integrating daily rates throughout the oviposition period (July and August). The total recruitment to each pond (no. eggs) was estimated from the product of annual oviposition rate and mean female fecundity. Fecundity was estimated from the mean size at emergence taken across all ponds and a size–fecundity relationship, because females had the potential to disperse among ponds. Sampling occurred only on calm, sunny afternoons, and fish and fishless ponds were alternately sampled to avoid bias in the assessment of recruitment rate with respect to pond type.

Data analysis

Where necessary, variables were $\log_e+1$-transformed to meet the assumptions of linearity, and normality and homogeneity of the error terms. All statistical analyses were performed using SYSTAT Version 7.0 (SPSS, Chicago Illinois, USA), SAS 8 (SAS In-

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stitute, Cary, North Carolina, USA), or G*POWER 2.0 (Faul and Erdfelder 1992).

To test whether larval abundance differed in ponds with and without trout, larval densities among ponds were compared using a repeated measures ANOVA. Trout presence or absence and year were tested as fixed effects, ponds were the repeated measure (random effect) over the two years of the study, and fixed effects (including Trout × Year) were tested using the pond(year) error term. Plant dry mass was included to statistically control for the effects of microhabitat on larval density within pond. Compound symmetry was used as the covariance structure. The effect of trout presence within each year was tested using post hoc linear contrasts.

The balanced dispersal model predicts that recruitment is significantly and positively related to emergence (McPeek and Holt 1992, Doncaster et al. 1997), and hence the associations between local adult emergence and recruitment of larvae were tested using Pearson correlations. No relationship is predicted for a source–sink metapopulation. Power calculations at $1 - \beta = 0.8$ and $\alpha = 0.05$ suggested that these tests had power to detect a relationship with a coefficient of determination of $r^2 \geq 0.373$ (Cohen 1988; but see caution by Hoenig and Heisey 2001).

Adult emergence and larval recruitment in fishless vs. trout ponds were compared with one-way ANOVAs. These ANOVAs had power to detect effect sizes ($\text{mean}_{\text{fishless}} - \text{mean}_{\text{trout}}/\text{SD}$; Cohen 1988) of 0.898 at $1 - \beta = 0.8$ and $\alpha = 0.05$.

To examine whether females selectively oviposited, patterns of oviposition density (females·m^{-2}·yr^{-1}) were used to generate hypotheses about potential cues used by females while ovipositing. Pond size, local pond population size of emerging adults, absolute area and percent cover of emergent sedges, and presence or absence of trout were used as predictors of oviposition density in forward stepwise multiple regression. Differences in pond size and local emergence could influence the number of females detecting a pond (i.e., large ponds may be more apparent), while the latter three factors could act as cues indicating pond quality (food, refuge from predators, presence of predators). Minimum tolerance was zero and α-for-entry to the model was 0.15. This model had power to detect an effect size of 0.696 (e.g., $F_{\text{crit } 1,10} = 2.431$) at $1 - \beta = 0.8$.

The source–sink model predicts that sources are net exporters of individuals and sinks are net importers (Pulliam 1988). The net production of adults for each pond was estimated using an Emigration Index (EI) that assumed closed pond populations. The EI was calculated at the pond-wide population scale as $\text{EI} = N_i - \text{E}(N_i)$ using the observed pond-wide population sizes of emerging adult females (N_i, 1997–1998 cohort) and the expected number of emerging females required to achieve observed larval recruit population sizes ($\text{E}(N_i)$, 1998–1999 cohort). Positive EI values represent the excess number of females emerging that could potentially disperse to other ponds, while negative values reflect ponds where emergence was insufficient to produce observed larval densities without immigration. Correspondingly, source patch $\text{EI} > 0$ and sink $\text{EI} < 0$, though knowledge of the local population growth rate is required to confirm the status of a patch as a source or sink. In a balanced dispersal model, all $\text{EI} = 0$.

The number of female recruits to pond i (1998–1999 cohort) can be estimated as $R_i = N_i \times f_i \times s_{\text{adult}}$, where N_i is the pond-wide number of adult emerging females (1997–1998 cohort) from pond i, s_{adult} accounts for terrestrial mortality, and f_i is the mean fecundity of adult females. Hence, the expected number of emerging females can be estimated as $\text{E}(N_i) = R_i/f_i \times s_{\text{adult}}$. R_i was the observed female pond-wide larval recruit population size, and mean fecundity was predicted from the regression equation $f = 1580.3 \times$ head capsule width $- 1667.7$, where head capsule width = mean head capsule width (mm) of BWP females emerging from pond i ($P < 0.001$, adj. $r^2 = 0.965$, $n = 7$, head capsule width data from Caudill and Peckarsky [2003]). The sensitivity of EI to changes in adult mortality ($= 1 - s_{\text{adult}}$) was examined using EIs calculated at the observed adult female mortality and several additional values ranging from 90% to 99%. For all observed values, numbers of females were estimated by dividing the total number of mayflies by two; there was no evidence of deviation from a 1:1 sex ratio in these populations (Caudill 2002).

Terrestrial survivorship of females in the 1997–1998 cohort was estimated for the regional metapopulation as $s_{\text{adult}} = \Sigma \text{ spent females}_i/\Sigma N_i$ for all 12 ponds; $i =$ 1–12, where spent females were the total number of spent females ovipositing per pond per year. The error associated with the estimation of adult female survivorship was assessed using a bootstrap analysis (Dixon 1993). For each of 5000 iterations, female adult survival was calculated by randomly sampling, with replacement, observed values of spent females and emerging females 12 times. A 95% confidence interval for adult survivorship was estimated with a percentile bootstrap (Dixon 1993). Iterations were programmed and run in MATLAB Version 5.3 (MathWorks, Natick, Massachusetts, USA).

Results

Fish populations

Ponds visually classified as fishless contained no trout. All fish sampled in the ponds were brook trout (*Salvelinus fontinalis*). Densities were reliably estimated in four of six trout ponds and ranged from 3.72 to 17.9 trout/100 m^2 (Table 1). Size of trout varied from 32 mm to 315 mm (fork length).

Patterns of larval abundance

Larval densities near the onset of emergence were significantly lower in trout ponds (repeated measures

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TABLE 1. Study pond elevation, area, and trout density in each of the two study years.

Pond	Elevation (m)	Area (m^2)	Trout density [no./100 m^2] (95% CI) 1997	1998
Avalanche	2890	683	0	0
Avery	3048	4676	⋯	0
Bellview	3030	773	0	0
Friends	2999	409	20.3 (20.0, 21.2)	17.9 (17.3, 19.1)
FS 401	3048	991	0	0
Gothic	2926	1182	4.65 (3.56, 6.52)	15.2 (13.9, 16.4)
Levy	2877	254	16.2 (15.4, 18.2)	6.7 (8.27, 11.4)
Marmot	2926	5726	⋯	0.175
Quigley	2984	484	4.34 (4.34, 4.75)	3.72 (3.72, 4.13)
Rustlers	2961	559	0	0
TxFsBr	2923	1180	8.5	7.12
UBBP	2920	1532	0	0

Notes: Trout densities at Marmot and TxFsBr could not be reliably determined, and the values given represent minimum densities based on the number of trout captured. Avery and Marmot ponds were not sampled in 1997.

ANOVA, $F_{1,10} = 13.37$, $P = 0.0044$; Fig. 3; see also Appendix A), suggesting potential differences in pond quality for mayfly larvae. Within ponds, density of larvae was significantly and positively related to plant dry mass ($F_{1,94} = 67.40$, $P < 0.0001$; Fig. 3). The effect of microhabitat was consistent between years and pond types (all $P > 0.05$), and there was no year effect ($F_{1,8} = 4.18$; $P = 0.0751$). The effect of pond type (trout, fishless) on larval densities was smaller in 1998 than in 1997 (Pond type × Year, $F_{1,8} = 5.81$, $P = 0.0425$), but was significant within both years (1997, $F_{1,8} = 13.94$, $P = 0.0058$; 1998, $F_{1,10} = 7.86$, $P = 0.0187$; Appendix A).

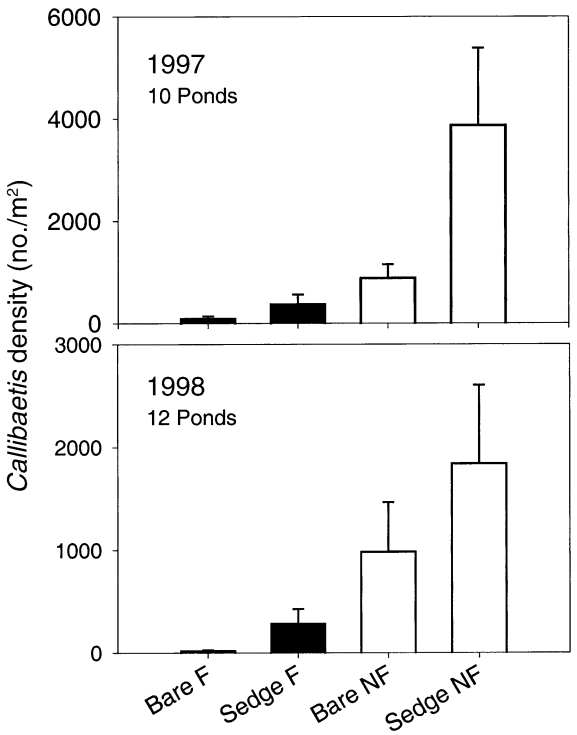


FIG. 3. Density of *Callibaetis* larvae (+1 SE) in two microhabitats, in ponds with and without fish, representing the extremes of plant structure within a pond. Five microhabitats were sampled in each pond each year. Only Sedge and Bare habitats are shown for clarity; these represent the samples within each pond with the most and least plant dry mass (a measure of habitat structure). Samples were taken in early summer before the beginning of adult emergence, in both years. Ponds are arranged by increasing trout density in 1998.

Emergence rates and recruitment in the sedge microhabitat

The best estimate of pond quality available for larval development was the emergence rate from the sedge microhabitat. In most ponds, nearly all the larvae in the 1997–1998 cohort emerged from the sedge habitat (overall, 92.5%), even though this habitat comprised only 12.9% of the total pond area. Within the sedge microhabitat, the rate of emergence varied from zero to 3898 individuals·m^{-2}·yr^{-1} among ponds (Fig. 4, top panel). Mean emergence rate of adults from the sedge microhabitat was greater from fishless ponds than from trout ponds by nearly an order of magnitude (mean fishless = 1881·m^{-2}·yr^{-1}, mean fish = 226·m^{-2}·yr^{-1}, $P = 0.029$, $F_{1,10} = 6.459$, $n = 12$, one-way ANOVA; Fig. 4, top panel).

Recruitment of larvae to the sedge microhabitat did not differ significantly between pond types, but was lower in ponds with trout (mean fishless = 3497 larvae·m^{-2}·yr^{-1}, mean trout ponds = 2163 larvae·m^{-2}·yr^{-1}; one-way ANOVA, $F_{1,10} = 1.125$, $P = 0.298$, $n = 12$; Fig. 4, top panel). Notably, the density of larval recruits at several trout ponds with few or no emerging adults was similar to the mean density across all ponds (e.g., TxFsBr, Levy, and, in particular, Gothic). Recruitment density in the sedge microhabitat for the 1998–1999 cohort was not related to local emergence rate of the 1997–1998 cohort ($P = 0.373$, $n = 12$, Pearson correlation; Fig. 4, top panel), consistent with the predic-

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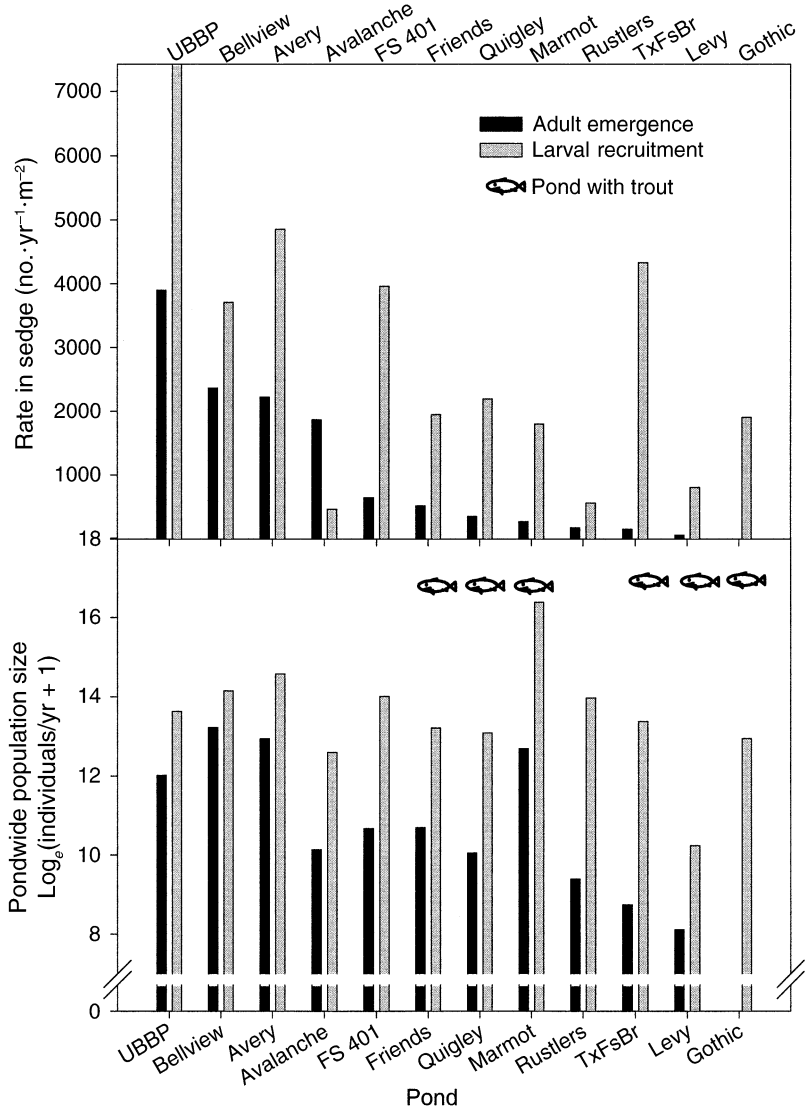


FIG. 4. The rate of adult emergence from the sedge microhabitat for the 1997–1998 cohort compared to the recruitment rate of larvae estimated using larval density for the 1998–1999 cohort in sedges (top panel), and at the pond-wide population scale (bottom panel; note $\log_e$ scale). There was no relationship between emergence and recruitment at either scale ($P > 0.05$). Ponds are arranged in order of decreasing adult emergence rate.

tions for a source–sink metapopulation, rather than a balanced dispersal dynamic.

Pond-wide population sizes of emerging adults and larval recruits

The pond-wide population size of emerging adults determined the contribution of each pond to the regional population of dispersing adults, and was determined by the size of the pond and the relative area of microhabitats within the pond, as well as the emergence rate from each microhabitat. Consequently, the mean pond-wide population size of emerging adults did not differ between pond types (one-way ANOVA, $F_{1,10} = 2.490$, $P = 0.146$, $n = 12$; Fig. 4, bottom panel), due to the large variance in pond size and relative cover of sedge beds. Similar to estimates of recruitment density in the sedge habitat, mean pond-wide population size of recruiting larvae did not differ between pond types (one-way ANOVA, $F_{1,10} = 0.535$, $P = 0.481$, $n = 12$). Most interestingly, and similar to estimates from the sedge microhabitat, pond-wide recruitment was not related to the pond-wide population size of emerging adults in the previous generation ($P = 0.142$, $n = 12$), consistent with the predictions for a source–sink metapopulation.

Oviposition behavior

There was no evidence that females selectively oviposited in ponds based on the presence of fish, pond size, area of sedge, relative coverage of sedge, or the

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TABLE 2. Estimation of adult female mortality using spent females collected after oviposition and emerging larvae (last instar larvae identified by the black wing pads) for the 1997–1998 cohort.

Pond	Spent females (no.)	Emerging females, 1997–1998 cohort (observed no.)
Fishless ponds		
Avalanche	372	12 763
Avery	2100	208 154
Bellview	115	275 825
FS 401	2362	21 465
Rustlers	619	5 961
UBBP	239	56 667
Ponds with trout		
Friends	168	22 103
Gothic	3218	0
Levy	530	1 668
Marmot	1542	162 047
Quigley	645	11 499
TxFsBr	1132	3 147
Total	13 041	781 299

Note: Terrestrial mortality = 1 − (spent females/emerging females)100 = 98.33%.

local population size of emerging adults (all $P > 0.05$, forward stepwise regression, $n = 12$). The lack of a relationship between oviposition and trout presence was consistent with the patterns observed in larval recruitment density.

Adult mortality and Emigration Index

Adult female survivorship was low (1.67% [95% CI: 0.80%, 4.97%], Table 2) relative to survivorship through all larval stages (9.8% for the metapopulation in the 1998–1999 cohort; Caudill 2002).

The Emigration Index (EI) suggested a large amount of migration among ponds. Some ponds had a high number of emigrants (EI > 0, potential sources, e.g., Bellview), while large numbers of females immigrated to other ponds (EI < 0, potential sinks, e.g., Gothic, Table 3). The sensitivity analysis of the EIs across an order of magnitude in variation in adult mortality (90–99%; Fig. 5, Table 3) suggested that the metapopulation would contain some sinks, and that one pond would remain a source (Bellview), even at high rates of adult mortality (99%). At the observed adult mortality rate (98.33%), only fishless ponds were exporters of females (sources). Notably, the EI within many ponds changed sign with increasing adult mortality values, indicating that variation in processes acting on adults in the regional terrestrial environment could influence the status of individual ponds as sources or sinks for larvae.

DISCUSSION

Habitat heterogeneity and dispersal can strongly influence population dynamics at both local and regional scales (Holt 1985, 1993, Pulliam 1988, Roughgarden et al. 1988, Nuernberger 1991, Palmer et al. 1996, Hanski and Simberloff 1997). A large body of theoretical work suggests that the magnitude of variability in patch quality and the dispersal system strongly affect metapopulation dynamics (Shmida and Ellner 1984, Pulliam 1988, Watkinson and Sutherland 1995, Boughton 2000; see reviews by Kareiva 1990, Hanski and Simberloff 1997, Diffendorfer 1998, Thomas and Kunin 1999). At present, few empirical studies have examined patch quality and dispersal simultaneously in the same metapopulation (Kareiva 1990, Harrison and Taylor 1997, Diffendorfer 1998; for an example, see Boughton 1999, 2000).

Here, patterns of adult production and subsequent larval recruitment were consistent with a source–sink metapopulation model with nonselective dispersal: ponds differed greatly in their quality (defined as the annual rate of adult production), females oviposited randomly with respect to pond quality, and net migration among ponds occurred. Thus, patterns of local larval abundance were determined by a combination of local (factors affecting larval survival) and regional (dispersal) processes.

Patterns of larval abundance

Larval density near the onset of emergence differed markedly among ponds in response to microhabitat within pond and the presence of trout predators. The reduction of larval density in trout ponds could have been generated by at least two qualitatively different mechanisms: (1) reduced survival of larvae in trout ponds, or (2) limited recruitment to trout ponds because of either spatial isolation or behavioral avoidance by ovipositing females.

There was little evidence of recruitment limitation or spatial isolation. Recruitment did not differ between pond types, and adult females did not strongly avoid ponds with trout, or select ponds that had high emergence rates. In fact, some ponds with little or no emergence of adults in the 1997–1998 cohort had high recruitment to the 1998–1999 cohort, qualitatively demonstrating net immigration to these ponds (e.g., Gothic, Friends Cut, Quigley; Fig. 4). Hence, differences in emergence from the sedge microhabitat probably reflected differences in larval survival rather than differences in initial recruitment.

Variability in patch quality

Population growth rate is the best indicator of local patch quality, although this property has been inferred using other measures such as local population size (e.g., Syms and Jones 2001). Unfortunately, population size is a potentially misleading surrogate in source–sink metapopulations because the majority of individuals can reside in sinks (Pulliam 1988, Pulliam and Danielson 1991). For instance, the emergence rate of adults from the sedge microhabitat was clearly lower in trout ponds, but the pond-wide population size of emerging adults did not differ between pond types (Fig. 4). In

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TABLE 3. Emigration index values by pond, across a range of adult female mortality values, including the observed value (98.33%).

Pond	Emerging females, 1997–1998 cohort (no. observed)	Females (no. expected)	Emigration Index adult mortality 90%	92.5%	95%	97%	98.33% (observed)	99%
Fishless ponds								
Avalanche	12 763	21 613	**9161**	**7961**	**5559**	**756**	−8849	−23 258
Avery	208 154	127 834	**186 848**	**179 746**	**165 543**	**137 135**	**80 320**	−4903
Bellview	275 825	94 979	**259 995**	**254 719**	**244 166**	**223 059**	**180 846**	**117 527**
FS 401	21 465	74 191	**9099**	**4978**	−3266	−19 753	−52 727	−102 187
Rustlers	5961	90 450	−9114	−14 139	−24 189	−44 289	−84 489	−144 789
UBBP	56 667	66 108	**45 649**	**41 976**	**34 631**	**19 940**	−9441	−53 514
Ponds with trout								
Friends	22 103	35 069	**16 258**	**14 309**	**10 413**	**2620**	−12 967	−36 346
Gothic†	0	28 569	−4761	−6349	−9523	−15 872	−28 569	−47 615
Levy	1668	1999	**1335**	**1224**	**1002**	**558**	−331	−1663
Marmot	162 047	828 493	**23 965**	−22 062	−114 117	−298 226	−666 445	−1 218 773
Quigley	11 499	57 031	**1994**	−1175	−7511	−20 185	−45 532	−83 552
TxFsBr	3147	47 215	−4722	−7345	−12 591	−23 083	−44 068	−75 544
Total	781 299	1 473 550	535 707	453 843	290 116	−37 340	−692 252	−1 674 618

Notes: The Emigration Index (EI) was calculated as the observed − expected number of females emerging from each pond. Expected values represent the number of emerging females needed to produce observed levels of recruitment, given female fecundity for closed populations. Ponds with EI > 0 were net exporters of females (putative sources, bold type), and ponds with EI < 0 were net importers of females (putative sinks).

† No emergence was observed at the Gothic pond, and the expected number of females was calculated using the mean fecundity of females in the metapopulation.

particular, the largest pond in the study (Marmot, with trout), had one of the largest pond-wide population sizes of emerging adults simply due to the large size of the pond and extent of sedge (Caudill 2002), and the pond had a large negative EI, suggesting it was a sink (Table 3). Thus, the use of population size to evaluate pond quality could be misleading. In this study, the best available estimate of patch quality was the emergence rate of adults from the sedge microhabitat (adults$\cdot$yr$^{-1}\cdot$m^{-2}), which was a reasonable approximation of population growth rate for the 1998–1999 cohort (Caudill 2002).

Trout may have reduced patch quality for larvae directly because trout frequently consume *Callibaetis* larvae (Luecke 1986, 1990, Carlisle and Hawkins 1998, Caudill 2002). At the extreme, one trout pond (Gothic) appeared to be a ''black hole'' sink, where no adults emerged (Fig. 4). The negative EI values in most trout ponds observed for a broad range of adult mortality rates (Fig. 5) were also consistent with the hypothesis that trout reduce habitat quality for *Callibaetis*. Furthermore, in the 1998–1999 cohort of *Callibaetis*, local population growth rate (λ) was negatively related to trout density. Nearly all ponds with more than approximately 1 trout 100/m^2 were sinks ($\lambda < 1$), while most ponds with few trout were sources ($\lambda > 1$; Caudill 2002).

Notably, the status of individual ponds as sources or sinks among years may depend on conditions encountered by adults in the terrestrial environment, assuming constant conditions within ponds. For example, interannual variation in weather conditions could cause individual patches to fluctuate between being sources and sinks by altering adult mortality rate among years (Fig. 5). This phenomenon may be common in organisms with complex life histories where mortality in the dispersal stages is high and variable (e.g., seeds, fishes and marine invertebrates with planktonic larvae, other aquatic insects; Roughgarden et al. 1988). Overall, the net negative EI suggested that the study ponds acted collectively as importers of females during the study period (Table 3). It is unknown whether immigration from other ponds outside the study system or sampling error in the estimation of EI for each pond produced this result.

Similarly, the status of individual patches as importers or exporters of females may fluctuate temporally, depending on interannual variation in recruitment, trout density, and other factors that affect larval growth and survival.

Dispersal among ponds

Comparison of emergence to recruitment and the EI calculations suggested females frequently migrated among ponds, because the observed recruitment at several ponds could not be accounted for by local emergence in the previous generation. The direct estimation of migration between Avery and FS 401 in summer 1999 further supports the conclusion of frequent dispersal in this species. A stable isotope enrichment mark–recapture experiment revealed that 17.5% of ovipositing females were immigrants at Avery, a pond with a high population growth rate in that year. In contrast, at nearby FS 401, a pond with a negative pop-

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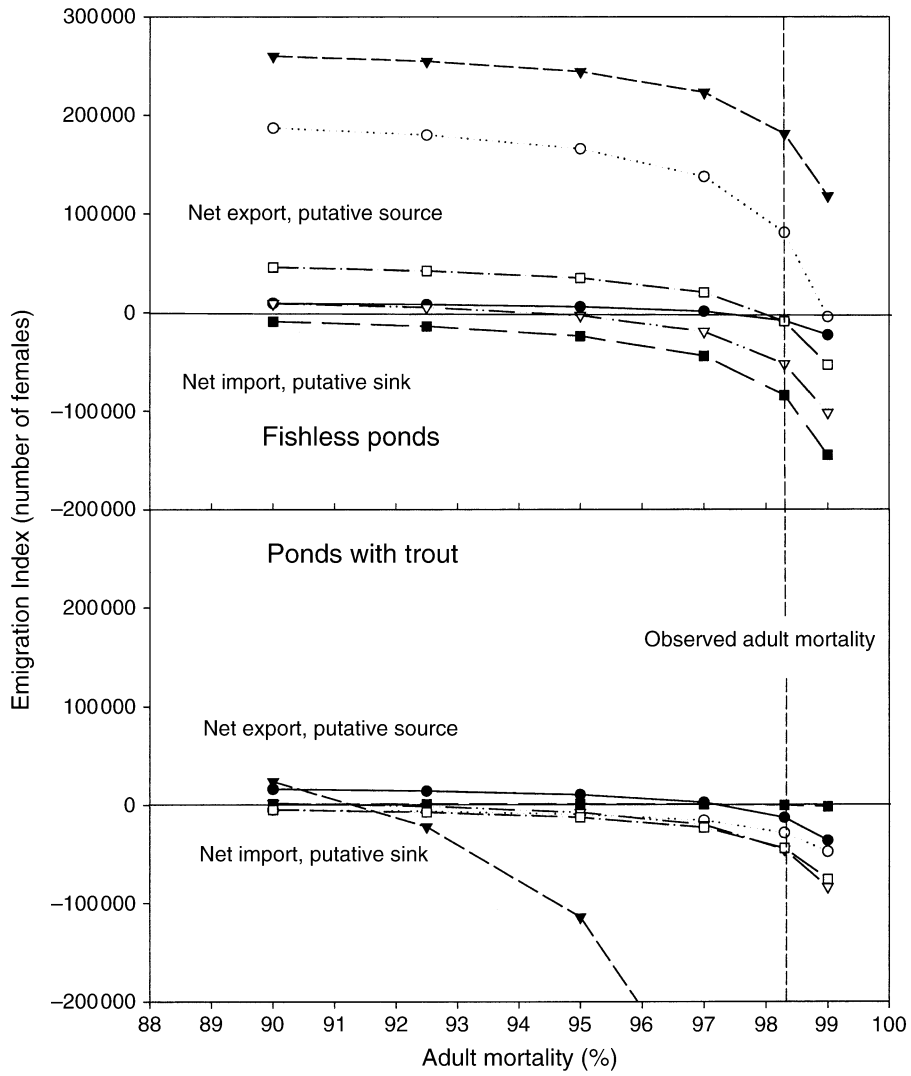


FIG. 5. Sensitivity analysis of the Emigration Index (EI) to variation in adult female mortality rate. Ponds above the horizontal line (EI = 0) were net exporters of females (putative sources), and those below were net importers (putative sinks), for a given rate of adult female mortality. All trout ponds were importers of females at the observed adult female mortality rate (98.33%, indicated by the vertical dashed line), while only two fishless ponds were exporters. Notably, the status of individual ponds as importers or exporters changed with differing rates of adult female mortality, suggesting that the status of ponds as sources or sinks may depend on conditions in the common terrestrial environment.

ulation growth, more than half of ovipositing females had immigrated from Avery (Caudill 2003). Since, by definition, ponds with negative EIs are importers of females, immigration to these ponds may have a strong affect on local population dynamics (e.g., populations in these patches may persist due to immigration), whereas the relative influence of immigration in ponds with large positive EIs is probably smaller. The mark–recapture data were consistent with this hypothesis, though in general, these predictions will depend on the exact distribution of female dispersal distances. Interestingly, dispersal among ponds has the potential to increase the variance in local population growth rate. Emigration from high quality patches may alleviate density dependent effects on growth rate, while immigration to low quality patches may depress local growth rate by elevating the larval population size above the local carrying capacity (e.g., Watkinson and Sutherland 1995).

In this metapopulation, the habitat experienced by adult females could be considered ''patchy'' (Harrison and Taylor 1997). In fact, recruitment in this system may approach a ''propagule rain'' (e.g., Harper 1977, Rabinowitz and Rapp 1980, Gotelli 1991), since recruitment was equal between pond types and not related to local production at any scale examined (Fig. 4). *Callibaetis* spp. frequently develop in temporary habitats (e.g., Berner and Pescador 1988) and possess several

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traits that appear to be adaptations to these habitats (e.g., ovoviviparous eggs). Hence, the high rate of migration among ponds observed may be related to past selection for vagile females that could rapidly colonize ephemeral habitats.

Complex life histories, the dispersal system, and metapopulation dynamics

The dispersal system of a species can strongly affect metapopulation dynamics (Harrison and Taylor 1997, Thomas and Kunin 1999, Boughton 2000). A balanced dispersal dynamic should occur if dispersing individuals visit and choose among several patches (i.e., ideal-free dispersal; Fretwell and Lucas 1970, McPeek and Holt 1992). Alternatively, three other dispersal systems can lead to source–sink dynamics. The source–sink concept was conceived for territorial species under the constraint of the ideal preemptive distribution (e.g., that individuals select the best, unoccupied habitat; Pulliam 1988, Pulliam and Danielson 1991). Passive dispersal (in the mathematical sense) occurs when a fixed proportion of a population emigrates from a patch each generation (Holt 1985). Diffusive dispersal occurs when organisms take a random walk through the environment, and immigration rates are expected to increase with increased patch size at a given distance (Kareiva 1985; reviewed in Boughton 2000).

Some dispersal systems were not supported by the patterns of emergence and subsequent oviposition and recruitment observed in *Callibaetis*. There was no evidence that *Callibaetis* achieved an ideal free distribution, nor was there evidence of a balanced dispersal dynamic, because oviposition and recruitment were not related to emergence and many EIs were much less than or much greater than 0. Ideal preemptive dispersal was unlikely in this species because there was little potential for social interactions among females during oviposition (Berner and Pescador 1988). Rather, the results suggest that *Callibaetis* dispersed among ponds in a ''passive'' rather than ''diffusive'' manner because oviposition rate did not increase with increasing pond size. Clearly, the source–sink dynamic observed here resulted in part from the lack of avoidance of low quality habitat.

The life histories, dispersal systems, and sensory capabilities of many organisms suggest that source–sink dynamics may be common in both freshwater and marine taxa. Several factors may lead to the dispersal of individuals to sink habitats including a high cost of sampling multiple patches, an inability to reliably predict patch quality from environmental cues during dispersal, and passive dispersal in a fluid medium.

Why were female *Callibaetis* unable to assess pond quality before oviposition? Mayflies appear to use primarily visual cues during oviposition and have been reported ovipositing on inappropriate surfaces such as pavement; apparently perceiving these surfaces as suitable oviposition habitat because of reflected polarized light (Kriska et al. 1998). Notably, visual cues may not be reliable indicators of trout status, which was probably determined by geomorphic position in the valley, rather than local pond features (Caudill 2002). Similarly, a high cost of dispersal may have contributed to the nonselective pattern of oviposition observed in *Callibaetis*. The relative rates of adult female and larval mortality in *Callibaetis* (98.3% vs. ~92%, respectively, Table 3; Caudill 2002) suggest that the costs of sampling multiple ponds may be high: while larval survival was lower in ponds with trout, death of an adult female before oviposition results in zero fitness. Thus, the optimal behavior for females may be to oviposit in the first pond they encounter during the oviposition flight, rather than attempting migration to multiple ponds in search of a high quality patch.

The fitness costs of sampling multiple ponds or sensory limitations appear to contribute to nonselective oviposition behavior in many other taxa. Female phantom midges (*Chaoborus crystallinus*) lose the ability to selectively avoid habitats with fish when dispersing greater distances, perhaps because of a deterioration in physiological condition or a perceived risk of death before finding suitable habitat (Berendonk and Bonsall 2002). Many aquatic insect taxa ''recruit'' to inappropriate habitat as winged adults (e.g., hemipterans, aquatic beetles) or during oviposition (e.g., mayflies). Inappropriate habitats include pavement (Kriska et al. 1998), car roofs (Fattig 1932, Belluck et al. 1980), and pools of oil (Horvath and Zeil 1996). Under more natural conditions, Morin (1984) observed 25 species of dragonflies ovipositing in a North Carolina farm pond, but only 11 species successfully emerged. Similarly, there was no evidence that two *Enallagma* damselfly species could discriminate between fish and fishless habitats when dispersing, despite high larval mortality in lakes with high fish density (McPeek 1990*a*, *b*, 1998). Another species, *E. ebrium*, probably displays a source–sink dynamic because adults frequently dispersed to fishless and winterkill lakes (lakes with low fish and dragonfly predator densities), but adults were only observed emerging from winterkill lakes (McPeek 1989). Hence, source–sink dynamics may be common not only in taxa with clear constraints on dispersal ability, but also in taxa such as adult insects that readily move through and seemingly can assess their environment.

In contrast, selective avoidance of low quality habitats (e.g., those with predators) may alter the metapopulation dynamic, shifting it from a source–sink dynamic to a balanced dispersal, ''classic,'' or mainland–island metapopulation dynamic (e.g., Berendonk and Bonsall 2002). Selective recruitment with respect to predator status of the habitat has been observed in several aquatic taxa including amphibians (e.g., Kats and Sih 1992, Holomuzki 1995), dipterans (Blaustein and Kotler 1993, Berendonk and Bonsall 2002), and an aquatic beetle (Resetarits 2001).

''Passive'' dispersal (in the biological sense), where displacement by transport in a fluid medium is large

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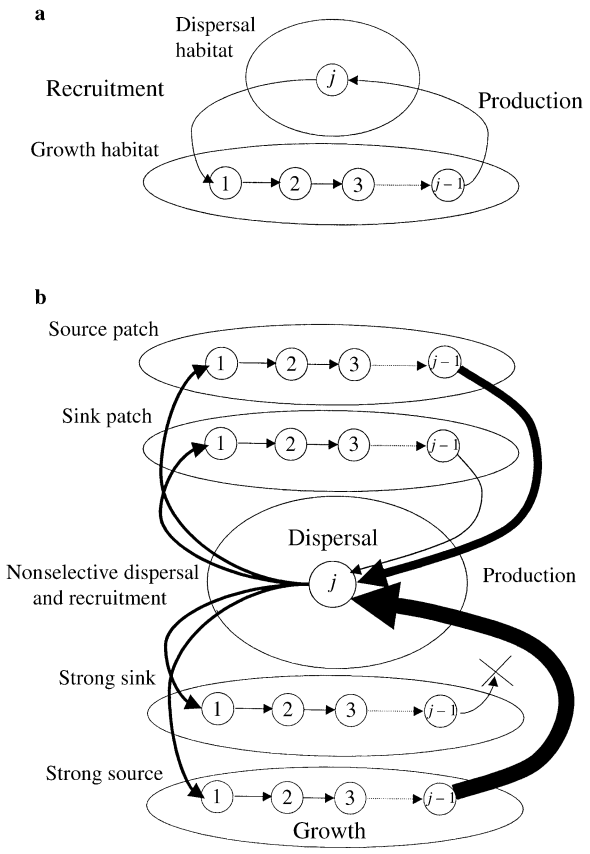


FIG. 6. (a) Traditional life cycle graph of a taxon with a relatively sessile growth stages (from 1 to $j - 1$) that produce a dispersing stage during reproduction (stage j; e.g., seeds, planktonic invertebrate and fish larvae, adult female insects carrying fertilized eggs). (b) Metapopulation model for the same taxon incorporating a spatially structured growth habitat that varies in quality and a single habitat where dispersal occurs (e.g., the water column for planktonic larvae or the terrestrial environment for adult aquatic insects). When patch selection is constrained (nonselective) and mobility is high, recruitment rates to all patches will be similar, despite large differences in the local production rates of dispersing offspring (indicated by arrows of varying widths).

relative to an organism's ability to select habitat or maintain spatial position, may also result in source–sink dynamics. Marine examples include the transport of zooplankton and the larval stages of benthic organisms out of estuaries and into coastal waters (e.g., Gaines and Bertness 1992, Plourde and Runge 1993, Zakardjian et al. 1999). Phytoplankton may be transported out of estuaries by horizontal advection or may sink vertically out of the photic zone (e.g., Zakardjian et al. 2000). At larger scales, ocean currents such as the Gulf Stream entrain warm water plankton communities and eventually carry large populations into habitat that is unsuitable. Cold slope-water masses can be also be carried offshore by Gulf Stream forcing, and the plankton in entrained water masses, including fish larvae, are likely doomed (Drinkwater et al. 2000). In a parallel fashion, lentic planktonic stages may be carried out of lake outlets, grow in lotic habitats, but are then unable to reproduce (e.g., Horvath and Lamberti 1999). Passive transport processes may affect lotic taxa as well. Drift of larvae in the water column may frequently carry individuals into sink habitats such as beaver ponds, lakes, and estuaries (e.g., Müller 1982). Longitudinal changes in the predation regime within watersheds may also produce source–sink dynamics. For example, *Ambystoma barbouri* salamander larvae frequently drifted into pools containing sunfish from fishless upstream habitats, and those drifting into pools containing fish had very low survivorship (Sih 1992, Sih et al. 1992, 2000).

Regional dispersal and differences in local patch quality may help explain the large variation in local population abundance and dynamics observed in many groups with complex life cycles (e.g., Roughgarden et al. 1988, Palmer et al. 1996). Local recruitment will frequently be decoupled from local production if dispersal is constrained (i.e., nonselective), if recruitment occurs from a regional population of nonreproductive dispersers, and if there is variability in patch quality during growth and reproductive stages (Fig. 6), as was the case for *Callibaetis*. Unfortunately, when mortality rates in sink habitats are high or the dispersing individuals are very small, such as in many marine taxa, the influence of sink habitats on regional populations will be difficult to detect. Nonetheless, better understanding how life history traits, dispersal, and variability in habitat quality interact will improve our ability to predict population dynamics in ''open'' systems.

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APPENDIX A

A table showing results of repeated measures ANOVA on *Callibaetis* larval density at the beginning of the emergence season in 1997 and 1998, and results of post hoc contrasts of fish vs. fishless ponds within year is available in ESA's Electronic Data Archive: *Ecological Archives* E084-050-A1.

APPENDIX B

A figure showing the density of ovipositing females in relation to local population size of emerging adults, pond size, and presence of trout is available in ESA's Electronic Data Archive: *Ecological Archives* E084-050-A2.

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