

Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): Effects of hydroperiod and salamanders

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Abstract

The absence of fairy shrimp (Anostraca) from permanent ponds and lakes is hypothesized to be the result of vertebrate predation. However, hatching cues for anostracan diapausing eggs include factors associated with the filling of temporary pond basins, and desiccation often increases the fraction of eggs that hatch. Thus, it is possible that in some species, eggs dispersed to permanent habitats never hatch, and vertebrate predation is not the proximate factor limiting distributions. We experimentally transplanted live egg-bearing females of the fairy shrimp *Branchinecta coloradensis* into permanent and temporary ponds in small chambers and allowed the chambers to overwinter in situ. There was no discernible effect of pond drying on hatching success (mean success = 50.9%). We also determined whether metamorphic salamanders (*Ambystoma tigrinum nebulosum*) could disperse viable fairy shrimp eggs by feeding on *B. coloradensis* in one pond and defecating in another. Hatching success for a salamander “ingested” treatment was estimated as 0.9%. Results of a third experimental treatment suggested that the eggs being carried by females were not fully mature, so that ingestion resistance might vary throughout the reproductive period of *B. coloradensis*. By combining these results with data on salamander movement and diet, we estimated salamander-mediated dispersal rates for fairy shrimp eggs. Metamorphic *A. tigrinum nebulosum* sp. are likely to be dispersing thousands of *B. coloradensis* eggs among ponds annually. Because our results demonstrate that dispersal between ponds can occur in large numbers, they support the prevailing hypothesis that vertebrate predators limited to permanent ponds are the proximate mechanism preventing the invasion of fairy shrimp.

Differences in community composition between temporary and permanent bodies of water can be striking, even when those communities are only a few meters apart. Large-bodied invertebrates commonly found in temporary ponds are conspicuously absent from neighboring bodies of water that do not dry (e.g., Williams 1987 and references therein; Batzer and Wissinger 1996; Wellborn et al. 1996). The crus-

tean order Anostraca exemplifies this pattern, and the factors that determine its distribution have been under investigation for at least the past 100 yr (e.g., Hay and Hay 1889; Avery 1939; Gallagher 1996).

Studies focusing on the distribution and ecology of temporary pond invertebrates have progressed in two general directions. First, it has become widely recognized that size-selective predation by vertebrates is an important determinant of community composition in freshwater systems (Brooks and Dodson 1965; Dodson 1974; Northcote 1988). The extreme rarity of Anostraca (fairy shrimp), Spinicaudata (clam shrimp), and Notostraca (tadpole shrimp) in permanent ponds and lakes is consistent with this hypothesis because predatory vertebrates are nearly ubiquitous in these systems, and the introduction of fish has been directly observed to cause the extinction of large zooplankton populations (Nilsson 1972; Parker et al. 1996).

In contrast to this recent focus on size-selective predation, many earlier investigators concentrated on the role of abiotic factors in preventing large zooplankton from actively invading permanent ponds and lakes. For example, some researchers hypothesized that diapausing fairy shrimp eggs might need to dry or freeze in order to hatch the following year (e.g., Hay and Hay 1889; Mozley 1932; Weaver 1943). If this were true, the presence of predatory vertebrates would not be solely responsible for the distribution of these zooplankton species. However, laboratory experiments on egg hatching in a number of species failed to provide any such

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generalizations, even though an osmotic change is necessary for the termination of diapause in most species (Avery 1939; Moore 1951; Brendonck 1996).

The most obvious approach to separating predatory and embryological factors is correlative, and in fact, Anostraca and other large Branchiopoda are occasionally found in permanent bodies of water where vertebrates are very rare or absent (Kerfoot and Lynch 1987 and references therein). However, habitat permanence and vertebrate predation covary so strongly as to preclude the separation of these factors from surveys alone in most regions. Here, we investigated the limitations to anostracan distributions in such a system.

We investigated vertebrate predation and invertebrate distributions at the Mexican Cut Nature Preserve, 17 km north of the Rocky Mountain Biological Laboratory in the Elk Mountains of Colorado (39.0°N, 107.1°W). The preserve contains closely spaced ponds on two plateaus on Galena Mountain at altitudes of approximately 3,400 and 3,450 m (the "Lower Cut" and the "Upper Cut," respectively). Pond sizes range between 15 and 4,600 m², with maximum depths of 0.3–2.5 m. Invertebrate distributions change markedly along hydroperiod gradients that covary with vertebrate predation (Dodson 1974; Wissinger et al. in press). More complete descriptions of the biota, hydroperiod, and chemistry of the ponds have been reported elsewhere (Sprules 1972; Wissinger and Whiteman 1992; Wissinger et al. in press).

Motivated by the variety of results obtained in laboratory hatching studies with anostracan eggs, we tested the impact of hydroperiod on *B. coloradensis* diapausing eggs in this field setting. Although size-selective predation has the potential to limit fairy shrimp distributions at this site (Sprules 1972), it is plausible that this potential is rarely realized because fairy shrimp eggs dispersed into permanent bodies of water do not hatch.

A second goal of the study was to quantify the dominant vector for fairy shrimp movement between ponds. There are few freshwater invertebrates for which dispersal has been quantified, and ecological studies addressing crustacean zooplankton dispersal are rare (e.g., Moore and Faust 1972; see discussion in Brendonck et al. 1990). In the Mexican Cut Nature Preserve, metamorphic adult salamanders can travel between ponds after feeding on fairy shrimp; thus, we attempted to quantify the dispersal rate of *B. coloradensis* eggs via salamanders. Although the prevalence of this mode of dispersal is unknown, it is quantifiable and may be of comparable importance in some areas to wind-, mammalian-, or avian-aided transport.

B. coloradensis distribution and abundance—Nine permanent and nine temporary ponds at the Lower Cut of the preserve were sampled one to four times each month during the ice-free season from 1990 to 1992. Some of the temporary ponds do not always dry completely and may be more accurately referred to as "semipermanent." However, for simplicity, all ponds in which surface area typically decreases by >95% annually will be referred to as temporary. The remainder, which dry very little, will be referred to as permanent. Zooplankton (including *B. coloradensis* nauplii) were collected with an 80- μ m mesh net thrown from the shore of each pond. In ponds too shallow for a zooplankton

net, samples were taken with a 2.2-liter Van Dorn sampling bottle mounted on a 1-m pole. Because fairy shrimp adults were occasionally observed to avoid the plankton net, visual censuses were made for the presence or absence of *B. coloradensis* adults weekly throughout the summer. In 1992, a plankton net with 20-mm Nitex mesh was also used to collect adults, and it appeared that *B. coloradensis* adults were unable to avoid this net. Because precise estimates of abundance were not essential for determining dispersal rates for *B. coloradensis* (see below), we present the range of adult densities (per liter) observed between 1990 and 1992 without regard to methodological biases.

We found that fairy shrimp distributions at the Mexican Cut Nature Preserve were associated with the presence or absence of branchiate (gilled) forms of *A. tigrinum* ($\chi^2 = 10.89$, 1 df, $P = 0.001$; Fisher's Exact Test $P = 0.003$), which covaries with pond permanence. Eight out of nine permanent ponds at the Lower Cut of the Mexican Cut Preserve contained paedomorphic salamanders and/or juveniles, and except for pond 9, fairy shrimp nauplii and adults were not collected in any of these ponds between 1990 and 1992 (Table 1). Fairy shrimp have also been absent from the same ponds in more recent samples (Wissinger and Bohonak pers. comm.).

Salamander life history and population censuses—Size-selective predation in the Mexican Cut ponds is complicated by the life history and mobility of the predators. Branchiate forms of the tiger salamander *A. tigrinum nebulosum* (larvae and obligately aquatic paedomorphic adults) are limited to permanent ponds, where they have the potential to affect zooplankton community composition (Sprules 1972; Dodson 1974). Metamorphic *A. tigrinum nebulosum* adults coexist with paedomorphs in this population, and feed actively in both permanent and temporary ponds. Analyses of gut contents have shown that metamorphs in temporary ponds contain an average of >70 adult fairy shrimp in their stomachs (Whiteman et al. 1994). Metamorphic salamanders in this population lay eggs in both permanent and temporary ponds (Wissinger and Whiteman 1992), and some of the hatchlings also prey on fairy shrimp (Wissinger et al. unpubl. data). Because both metamorphs and hatchlings coexist with and prey on *B. coloradensis* in temporary ponds, the simple presence or absence of predatory vertebrates is clearly not the sole determinant of anostracan distribution in this system.

We monitored the salamander population weekly or bi-weekly throughout the ice-free season from 1990 to 1996. Salamanders were captured by hand or by using dip nets, and they were identified visually to age class or morph (by body size and the presence or absence of larval characters such as gills and tail fin). Each individual was marked with unique toe clips (1-yr class larvae and older) or cohort tail clips (hatchlings). Repeated mark and recapture permitted the calculation of relative densities for each life-history stage in each pond, as well as estimates of metamorphic adult movement rates throughout the pond system. Recapture data showed that essentially all metamorphs in the population were marked (see also Whiteman et al. 1994).

From 1990 to 1996, 96 movements of metamorphs were recorded between ponds within the same season. Of these

Table 1. Hydroperiod and distributions of *A. tigrinum nebulosum* and *B. coloradensis* in 19 ponds of the Mexican Cut Nature Preserve. Salamander distributions are from data collected during 1990–1996, and fairy shrimp distributions represent adult densities during 1990–1992. “P” represents present, while “(P)” represents low relative abundances (≤ 1 adult or ≤ 10 larvae).

Pond	Hydroperiod	<i>B. coloradensis</i> (liter ⁻¹)	Salamander morphs present			
			Metamorphs	Paedomorphs	0-yr class larvae	1 ⁺ -year class larvae
1	Permanent	0	P	P	P	P
2	Permanent	0	(P)	P	(P)	P
3	Permanent	0	(P)	P	(P)	P
4	Permanent	0	(P)	P	(P)	P
5	Permanent	0	P	P	P	P
9	Permanent	0.02–0.80	P		P	
12	Permanent	0	P	P	P	P
14	Permanent	0	(P)			
18	Permanent	0	(P)	(P)		
6	Temporary	0.01–0.10	P		(P)	
7	Temporary	0.20–0.50	P			
8	Temporary	0.20–2.0	P		P	
10	Temporary	0.07–0.10	P		(P)	
11	Temporary	0.10–0.13	P		(P)	
13	Temporary	0.2–2.1	P			
15	Temporary	0.07–1.1	P			
16	Temporary	0				
18a	Temporary	1.0–2.5				

movements, 13% (12 migrations) were from ponds containing fairy shrimp to permanent ponds lacking them (Table 2). Because ponds were sampled only weekly or biweekly throughout the ice-free season, these estimates may be conservative.

Design of field experiments—To determine hatchability of *B. coloradensis* diapausing eggs in permanent and temporary ponds, we collected fairy shrimp females from temporary pond 8 and experimentally transplanted them into five permanent ponds (ponds 1, 5, 9, 12, and 14) and five temporary ponds (ponds 8, 10, 11, 13, and 15) on 15 August 1993. By this date, diapausing eggs were being carried externally in brood sacs by *B. coloradensis*.

A “live” treatment consisting of five *B. coloradensis* females bearing diapausing eggs was transplanted into each

destination pond in a single 50-ml plastic snap-cap vial. (*B. coloradensis* has nonoverlapping generations, with propagules hatching only after a dried pond refills. As a result, we assumed that the females in these chambers would die before their offspring hatched.) The center from the cap of each vial had been removed, and an oversized piece of 60- μ m mesh was placed underneath the cap as it was closed. Each vial was sealed with hot glue, creating an experimental chamber through which water, bacteria, and some algae could pass but one that would retain all life-history stages of *B. coloradensis* (eggs $\approx 300 \mu$ m in diameter). Except for a brief transfer using soft tin forceps, females and their eggs were kept underwater during the entire process. To estimate the number of eggs put into each vial, clutch size was determined at the start of the experiment for 42 randomly chosen *B. coloradensis* females.

Because *B. coloradensis* females carry their eggs externally in a brood sac, an “ingested” treatment was used to determine the hatchability of *B. coloradensis* eggs after the female had been eaten by a salamander. Twelve *A. tigrinum nebulosum* metamorphs were captured on 5 August 1993 and held in individual containers with rocks and ≈ 2 liters of pond water at ambient water temperature (17°C) at the field site. The salamanders were fed only *B. coloradensis* males for the next 5 d to clear their guts of any previously eaten egg-bearing females. (Gut passage time for captive salamanders varies between 2.7 and 6 d: Jaeger and Barnard 1981; Gabor and Jaeger 1995). All fecal matter was discarded daily.

On 10 August, each salamander was fed six egg-bearing *B. coloradensis* females. Fairy shrimp were swallowed whole, and we did not observe any eggs dislodged during the feeding process. Following this, salamanders were again

Table 2. Within-year movements of *A. tigrinum nebulosum* metamorphs between ponds during 1990–1996 at the Mexican Cut Nature Preserve.

Origin pond	Destination pond		
	Permanent, no fairy shrimp	Permanent, fairy shrimp	Temporary, fairy shrimp
Permanent, no fairy shrimp	5	2	36
Permanent, fairy shrimp	2	0	22
Temporary, fairy shrimp	10	7	11
Temporary, no fairy shrimp	1	0	0

fed only fairy shrimp males for another 5 d. On 15 August, we assumed that all *B. coloradensis* eggs that were eaten had been passed, and salamander feces from the last 5 d of the experiment were collected. Fecal matter from each salamander was placed into separate plastic vials and transplanted into one of the 10 ponds described above. Feces from the remaining two salamanders were preserved in ethanol for later analysis.

In some Anostraca, development of the diapausing egg outer shell occurs in the ovisac (e.g., Brendonck 1991). This suggests that differences in hatching between the ingested and live treatments could be due to interruption of egg development by the ingestion process. Further, ingestion resistance could vary temporally, with increased resistance as the summer progresses and the eggs mature. To specifically investigate the effect of developmental termination, we set up an additional "removed" treatment, where the ovisacs from *B. coloradensis* females were removed by pinching them off with forceps at the proximal end. This did not damage the eggs physically, and they were only out of pond water for the brief period of transfer. Five ovisacs were placed into each of 10 vials, which were then put into the five temporary and five permanent ponds as described above.

The three vials for each treatment were confined to a jar with coarse window screening in place of the lid. Each jar was placed in the center of the pond, where it remained until 12 June 1994, when the vial contents were preserved in 70% ethanol. Fairy shrimp eggs and nauplii were later counted under a dissecting microscope.

Estimation of egg input for B. coloradensis hatching experiments—The initial conditions in each experimental chamber were estimated using *B. coloradensis* females preserved at the initiation of the experiment. The mean number of eggs carried by each female was 18.7 ± 3.2 (SD, $n = 42$, range = 9–25), but because the distribution was non-normal, we conducted computer simulations to estimate the mean number of eggs placed into each treatment and the variance around that mean. Five hundred groups of five egg-bearing females were drawn at random with replacement to estimate that 93.6 ± 6.6 (SD) eggs were placed into each chamber for the live and removed treatments (range = 69–115). In a similar way, it was estimated that 112.4 ± 7.1 (SD) eggs had been fed to each metamorph, and this was used as probable input for the ingested treatment ($n = 500$ bootstraps, range = 93–135).

Recovery of eggs from experimental chambers and salamander feces—The estimated numbers of eggs placed into each chamber were used to convert the numbers of eggs and nauplii recovered when the experiment ended into percentages of the probable inputs. Although only the percentage of hatched nauplii is relevant for comparison among the three treatments, the number of eggs recovered provided a way of verifying our input estimates. Because hatched eggs, unhatched viable eggs, and unhatched inviable eggs could not be reliably distinguished, only the total number of eggs recovered from each treatment is reported here.

The 10 live treatment chambers contained a mean of 86.6 ± 12.7 eggs (SD, range = 68–103), and the 10 removed

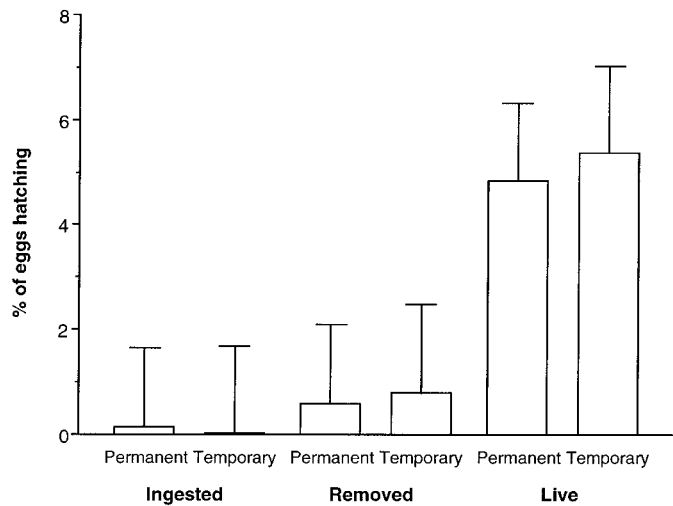


Fig. 1. Percent (± 1 SE) of *B. coloradensis* diapausing eggs hatching in five permanent and five temporary ponds following digestion by salamanders, after transplanting live females, and after transplanting egg sacs that had been manually removed from females.

treatments contained 47.4 ± 19.5 eggs (SD, range = 22–71), which corresponded to 92 and 51% of the estimated input, respectively. Between 3 and 390 *B. coloradensis* eggs were recovered from the 10 ingested treatments (142.5 ± 138.4 , SD), and 3 of the 10 contained considerably more than the 112.4 eggs estimated as input. The two extra salamanders for which feces were preserved contained 77 and 301 eggs, of which the latter was greater than the maximum obtained from the 500 simulations described above. From these data, we concluded that the guts of at least some salamanders were not completely cleared before the experiment began. Nonetheless, we judged 112.4 eggs to be the most appropriate input for calibrating the proportion of fairy shrimp eggs that hatched following gut passage.

There were no differences between permanent and temporary ponds in the number of eggs recovered from each experimental chamber (*t*-test on square root [eggs], $t_{26} = 0.65$, $P > 0.5$; square root transformation used to meet normality assumptions).

Hatchability of B. coloradensis diapausing eggs—In the transplant experiment, fairy shrimp nauplii hatched in every pond except pond 14. Overall, 50.9% of the eggs in the live treatment hatched, followed by 7.0% in the removed treatment and 0.9% in the ingested treatment (Fig. 1). However, there were large numbers of treatment \times pond combinations with no hatching at all (13 out of 30), and there was unequal variance among the three treatments (squared ranks test, $P < 0.001$, $T = 20.7$, 2 df; $P < 0.05$ for all post hoc contrasts; Conover 1980). Because of this, results of the experiment were interpreted using nonparametric Friedman tests, modified to account for multiple ponds within each permanence-treatment combination (Marascuilo and McSweeney 1977). Percent of eggs hatching within each pond was dependent on treatment ($T = 13$, $0.005 > P > 0.001$), but not on pond permanence ($T = 0.091$, $P > 0.25$, 1 df). Post hoc contrasts

showed that treatment significance was due to greater hatching in the live treatment than in the ingested and removed treatments (Marascuilo and McSweeney 1977, $\alpha = 0.05$).

Quantifying fairy shrimp transport via salamander vectors—From these experiments and behavioral observations, we calculated a dispersal rate for *B. coloradensis* eggs via salamanders that feed in temporary ponds, move over land, and defecate in a neighboring pond. Because our primary interest was in community composition differences, we calculated the number of immigrants into ponds lacking fairy shrimp as well as into ponds that contained fairy shrimp. Five parameters were estimated to arrive at these dispersal rates: (1) movement rates of salamanders, (2) number of fairy shrimp per salamander gut, (3) fairy shrimp sex ratio, (4) fairy shrimp clutch size, and (5) percent of ingested eggs that hatch. A limited sensitivity analysis was conducted by calculating both a mean and a maximum estimate for each parameter.

Because 12 salamanders were observed to move from ponds with *B. coloradensis* to ponds lacking *B. coloradensis* during 7 yr of monitoring (Table 2), we inferred that on average, 1.7 salamanders made such a journey each year. A 95% confidence interval around the mean included 3.6 as the upper limit, which was used for the maximum dispersal estimate. From the raw data of Whiteman et al. (1994), we calculated a mean of 73.5 fairy shrimp per gut from metamorphs in ponds containing *B. coloradensis* ($n = 38$) and an upper and lower 95% confidence limit of 50.2 and 97.0, respectively. Assuming an average sex ratio of 0.5 (unpubl. data), this translates to a mean of 36.8 females per gut. Mean clutch size for fairy shrimp females (18.7) was taken from the experiment above, and a maximum estimate of 25 eggs per female was used. This represented the highest number of eggs in the 42 individuals examined.

For simplicity, the movement events were assumed to occur instantaneously (i.e., all gut contents were deposited in the destination pond). We have frequently observed *A. tigrinum nebulosum* traveling between ponds on rainy nights but only occasionally during the day. Accordingly, we hypothesize that migration events almost always take place within a single night. The average distance between all ponds at the site is <100 m, and neighboring ponds are almost always <10 m apart. Furthermore, the time for gut passage in salamanders varies between 2.7 and 6 d (see above). Thus, it is likely that movement time between ponds is negligible in comparison with gut passage time.

Using this assumption, we estimated that approximately 1,180 *B. coloradensis* eggs were moved each year by salamanders at the Mexican Cut Preserve into ponds lacking *B. coloradensis*, with a maximum estimate of 4,389. An additional 40 salamanders moved among ponds containing fairy shrimp during the 7 yr of the study (Table 2); using the same formulas, these accounted for an additional 3,932 eggs moved annually (estimated maximum of 7,334). With the hatching success of 0.9% obtained in the above experiment, the total of 5,112 eggs translates to ≥ 45 viable *B. coloradensis* propagules dispersed annually between all of the ponds at the Mexican Cut Preserve by salamanders. Of these, 10.5 ($=1,180 \times 0.9\%$) are deposited in permanent

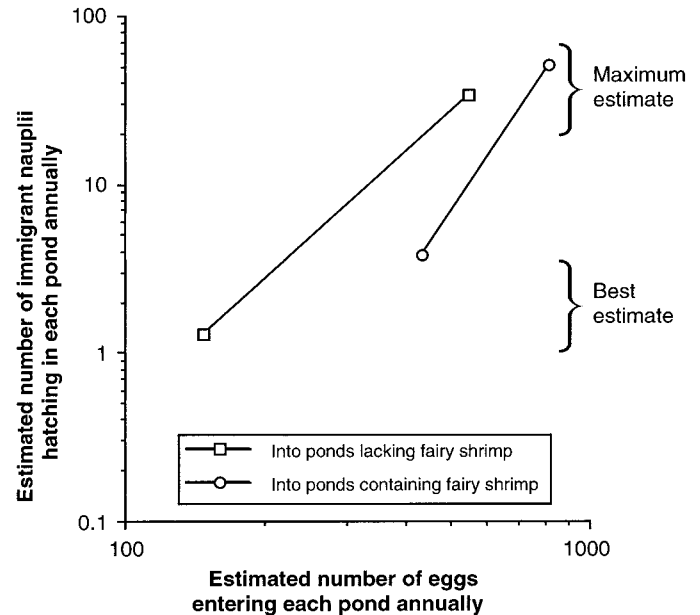


Fig. 2. Estimated number of viable *B. coloradensis* nauplii moved annually into each pond at the Mexican Cut Nature Preserve by *A. tigrinum nebulosum* metamorphs, as a function of the estimated number of eggs moved. The lower number for each category represents the best estimate, and the upper represents a maximum (see text for details).

ponds lacking fairy shrimp. For the maximum estimated dispersal rates of viable nauplii, the maximum egg estimates were multiplied by 6.2%, which was the highest hatching rate from any of the 10 ponds in the experiment above. This yielded an upper limit of 730 viable nauplii dispersed annually between all ponds by salamanders, with 273 of these hatching in permanent ponds lacking fairy shrimp in plankton samples.

Because there are nine ponds containing fairy shrimp (Table 1), these dispersal estimates translate into 436.9 eggs and 3.9 nauplii immigrating into each fairy shrimp pond annually (maximum of 814.9 eggs and 50.7 nauplii per pond; Fig. 2). The calculations outlined above yield an estimate of 147.5 eggs entering each of the eight permanent ponds that lack fairy shrimp (maximum of 548.6 eggs per pond; Fig. 2). An average of 1.3 of these hatch the following spring in each permanent pond (34.2 maximum).

There are three conclusions from our study. First, there was no significant effect of pond permanence on the hatchability of *B. coloradensis* diapausing eggs (Fig. 1). This suggests either that hatching in this species is cued by factors other than water chemistry (e.g., photoperiod or water temperature) or that permanent ponds at the site experience changes in water chemistry that promote hatching. These ponds generally experience a decline in conductivity and pH early in the spring (Wissinger and Whiteman 1992) when diapausing eggs hatch. Furthermore, oxygen concentrations in ice-covered ponds can often reach low levels during the winter (Mossin 1986; Devito and Dillon 1993), which would be elevated when the ponds are flushed following ice-out.

In contrast to our results, studies of some Anostraca have

suggested or demonstrated reduced hatching when eggs do not dry (*see* Brendonck 1996). For example, Broch (1965) collected eggs of the anostracan *Chirocephalopsis bundyi* along a transect from the edge to the center of a temporary pond, sampling numerous times as the pond dried. In combination with laboratory experiments, his data showed that embryological development in this species is arrested at three separate points that coincide with changes in pond hydroperiod. Broch concluded that diapausing eggs of this species would not hatch in ponds without fluctuating water levels. It is possible that in species such as *C. bundyi*, diapausing eggs that arrive in permanent bodies of water lie dormant in the sediment and eventually die.

Second, many more eggs hatched in the live treatment than in the removed or ingested treatments, and the two latter treatments were not significantly different from each other (Fig. 1). This suggests that eggs in this species may continue to develop after release into the brood sac, as has been described in other anostracans (Brendonck 1991). Although we did not conduct a detailed embryological study, we suspect that digestion resistance may increase later in the season or in previously shed eggs that are incidentally ingested by benthically foraging salamanders. However, it is clear that *A. tigrinum nebulosum* is capable of passing at least some viable anostracan eggs. Although the prevalence of this phenomenon in salamanders is unknown, the resistance of crustacean eggs to gut passage has been well established for a variety of other vertebrates and invertebrates (Mathias 1937; Proctor et al. 1967; Moore and Faust 1972; Mellors 1975; Castro et al. 1989; Redden and Daborn 1991).

Third, our results show that diapausing eggs of *B. coloradensis* are capable of being transported to permanent ponds by salamanders and that at least some of these eggs can hatch the following year. Although the role of nonamphibian vectors has not yet been investigated at this site and the errors in our dispersal estimates are not completely known, we believe that an estimate of 1–30 viable eggs dispersing into each permanent pond annually is reasonable. Population genetic studies of *B. coloradensis* in the region revealed very low genetic differentiation among local ponds, and gene flow estimates were remarkably similar to the dispersal estimates obtained here (gene flow estimated as 1.3–4.0 individuals per pond per generation; Bohonak in press). The data in Whiteman et al. (1994) contain an additional observation that supports our general conclusion. In that study, the gut contents of 1 out of 20 metamorphs captured in permanent ponds contained 149 fairy shrimp. This individual was undoubtedly a migrant from a temporary pond.

Quantitative estimates of fairy shrimp dispersal complement the results of predation experiments at this site. Branchiate morphs of *A. tigrinum nebulosum* consistently exhibit high electivities for *B. coloradensis* adults in experiments (e.g., Sprules 1972; Whiteman et al. 1996). However, the conclusion that branchiate salamanders limit this species' distribution requires a plausible mechanism for the dispersal of viable propagules. Estimates of dispersal also provide the data necessary for assessing the biological significance of size-selective predation in the field. For example, high electivities by vertebrate predators may be largely irrelevant in ponds too remote to receive dispersing propagules.

Correlational data on zooplankton distributions, vertebrate distributions, and hydroperiod are insufficient to test mechanistic hypotheses, often yielding a number of plausible alternatives. This is particularly true for permanence gradients in freshwater ecosystems, because vertebrate predators covary strongly with hydroperiod, and it is difficult to find comparable ponds and lakes that vary in the presence of fish or amphibians (Wellborn et al. 1996). Even in the Mexican Cut Nature Preserve, where this correlation is not perfect (Table 1), definitive answers are not possible without additional experiments. For example, pond 9 (Table 1) could potentially provide evidence relevant to the limitation of *B. coloradensis* to temporary ponds by vertebrates because it lacks paedomorphs and larvae (except for hatchlings). However, some or all of the fairy shrimp in pond 9 are likely to be annual immigrants, because it receives considerable inflow from temporary pond 10 during snowmelt each spring. Furthermore, *B. coloradensis* does not inhabit all ponds with low densities of predatory salamanders or ponds that lack salamanders completely (Table 1). Thus, our verification that the diapausing eggs of this anostracan can actually hatch in ponds where the species has not been found historically is essential support for the hypothesis that branchiate forms of *A. tigrinum* are the proximate factor limiting the local distribution of *B. coloradensis*.

It seems remarkable that hundreds of *B. coloradensis* nauplii may hatch annually in ponds from which these animals have never been collected. However, this result confirms that active elimination of fairy shrimp from permanent ponds at the Mexican Cut Preserve is likely to occur frequently. On an annual basis, the absence of *B. coloradensis* adults from any particular pond may be due to a lack of viable propagules, but over multiple years, the arrival of viable *B. coloradensis* eggs is probably a statistical certainty. Our findings complement those of Sprules (1972), who showed experimentally that adults of this species are capable of living in permanent ponds and that paedomorphic *A. tigrinum nebulosum* are capable of eliminating them quickly. Thus, ongoing predation by branchiate salamanders is of paramount importance in structuring these permanent pond communities.

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