

Movement of logperch—the obligate host fish for endangered snuffbox mussels: implications for mussel dispersal

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Abstract Unionid mussels are highly imperiled and the survival of their local populations is linked to the availability and dispersal potential of their host fish. We examined the displacement distance of logperch (*Percina caprodes*), which are obligate host fish for endangered snuffbox mussels (*Epioblasma triquetra*), to determine the dispersal potential by fish. Logperch in the Sydenham River, Ontario, Canada, were electrofished and marked with visible implant elastomer on five sampling dates during the gravid period of *E. triquetra*. The majority of all recaptures (82%) of *P. caprodes* occurred within 30 m of their original capture location, with a mean displacement distance of 13 ± 3 m (mean \pm standard error, $n = 28$). These results were consistent with a review of movement studies of small benthic host fish (i.e., darters and sculpins), which revealed average fish displacement distances of 37 ± 19 m ($n = 14$ species; range: 4–275 m). However, significantly greater movement distances were also found and the maximum displacement distance increased significantly with the spatial extent of the study and with the duration of the study. These results indicate that many *P. caprodes* remain in a small area, which could restrict

the dispersal and (re)colonization potential of *E. triquetra*. Further studies are needed to determine the dispersal potential of mussels via host fish, which may be important for maintaining the connectivity among unionid populations.

Keywords Freshwater mussel · *Percina caprodes* · *Epioblasma triquetra* · Unionidae · Connectivity · Small benthic fish

Introduction

Freshwater mussels are among the world's most imperiled taxa (Lydeard et al. 2004), and over 70% of species (Unionidae and Margaritferidae) in North America have experienced declines (Williams et al. 1993). In some cases, these declines can be attributed directly to the absence of fish hosts on which unionoid mussel larvae (glochidia) are parasites (McNichols et al. 2010); e.g., when a dam blocks the migration of a host fish (Kelner and Sietman 2000). In addition to serving as hosts for glochidia, fish also act as their agents of dispersal. Dispersal is fundamental for the functioning of a meta-population (Hanski 1999, Crone et al. 2001, Ovaskainen and Hanski 2004), and determines the connectivity among mussel beds, which are dense multi-species assemblages where densities are 10–100 times higher than outside of those beds (Vaughn 1997; Strayer et al. 2004; but see Box et al. 2002). However, little is known about dispersal rates in unionid mussels (Strayer 2008). Results of genetic studies using microsatellites suggest that gene flow among mussel populations can be limited and dispersal restricted (Kelly and Rhymer 2005; Wolfe et al. 2007).

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Unionid mussels have developed a fascinating array of strategies to attract and infest host fish with their glochidia (Barnhart et al. 2008), many of which may affect their dispersal abilities. For example, mussels of the genus *Epioblasma* have a specialized system in which the host is captured between the mussel's valves before it releases its glochidia (Barnhart et al. 2008). The vast majority of identified host fish (i.e., metamorphosis observed in laboratory infestations) for *Epioblasma* species are small benthic fish, darters and sculpins in particular (Cummings and Watters 2005). The dispersal potential of unionid mussels depend on the movement of their host fish during the parasitic larval stage.

E. triquetra (Rafinesque, 1820), the snuffbox, is an excellent model organism in which to examine the dispersal potential via a host fish, since it is believed to be specialized on one host fish, the logperch, *Percina caprodes* (Rafinesque, 1818), as shown in laboratory and field studies (Sherman 1994; McNichols 2007; Barnhart et al. 2008). The sturdy skull of *P. caprodes* enables the fish to survive capture by the mussel, whereas the skulls of *Etheostoma* species can be crushed (Barnhart et al. 2008). *E. triquetra* is dioecious and sexually dimorphic, and females are long-term brooders (bradytictic), with fertilization occurring in late summer and host infestation occurring the following spring or summer (Clarke 1981; Sherman 1994). The species is endangered in Canada, and is vulnerable globally (Morris and Burridge 2006).

The movement of large fish such as salmonids has been well studied, but information on the movement of smaller fish such as darters and sculpins is less complete (Neely and George 2006). The consensus among a number of these studies is that the movement of smaller benthic fish is limited (Freeman 1995; Petty and Grossman 2004; McLain and Ross 2005), although larger movement distances have

also been reported (Labbe and Fausch 2000; Roberts and Angermeier 2007; Roberts et al. 2008). Unfortunately, there is a dearth of information about the movement behavior and home ranges of *P. caprodes*. This study, therefore, examines the displacement distance of *P. caprodes*, which is a first step towards a better understanding of the dispersal of endangered *E. triquetra*.

Methods

Study area

The study was undertaken in a 135-m long 4th order reach in the east branch of the Sydenham River in southwestern Ontario, Canada (42°37'35"N, 82°1'23"W), one of the few sites where *E. triquetra* still occurs in Canada (~0.04 mussels m⁻², Metcalfe-Smith et al. 2007). Twenty-three of the 30 unionoid species currently known in the Sydenham River occur in the study reach, and it has a high overall density of ~11 mussels m⁻² (Metcalfe-Smith et al. 2007). The daily discharge (Q) ranged from 0.344 to 200 m³ s⁻¹ between 1998 and 2007, with a mean of 10.80 m³ s⁻¹ (Environment Canada, 2009). During the sampling period in late August to mid October 2007, Q ranged between 0.635 and 1.42 m³ s⁻¹ (Table 1), the width of the river ranged between 15 and 25 m, and the midstream water depth ranged between ~20 and 50 cm. The reach consisted of riffle and run, dominated by a mixture of gravel (38.3%), sand (28.3%), and cobbles (20%), with some clay (8.3%) and boulders (5%). In-stream fish habitat consisted of large-rock cover, with some macrophytes. The riparian vegetation was largely meadow (e.g., *Urtica dioica*) on top of soft sloping clay banks, with immediate adjacent shoreline vegetation (1.5 m from shore) largely intact (~75%).

Table 1 Summary of number of *P. caprodes* marked, recaptured, the measured displacement distances, estimated turnover rate, time between mark and recapture, and daily discharges on sampling dates from late August to mid October 2007

Week	Date	Duration (interval) (days)	No. newly captured (unmarked)	No. recaptured	Total	Displacement Mean \pm SE (range) (m)	Turnover rate (/month)	Time between mark and recap. of. ind. (weeks)	Daily discharge (m ³ s ⁻¹)
0 ^a	27 Aug	0	29	n/a	29	n/a	n/a	n/a	1.42
2.4 ^a	13 Sep	17	28	1	29	0	n/a	2.4	0.936
4 ^a	24 Sep	28 (11)	42	2	44	15 \pm 0	0.37 (1.00/month)	1.6	0.653
5.4	04 Oct	39 (10)	76	8 ^b	84	13 \pm 7 (0–45)	0.32 (0.95/month)	1.4–5.4	0.714
7.4	18 Oct	52 (14)	31	17 ^c	48	13 \pm 4 (0–75)	0.32 (0.68/month)	2–3.4	0.726
	Total	52 (52)	206	28	234	13	0.3 (0.18/month)	n/a	n/a

^a Fish were only captured in three home sections

^b One fish had been recaptured previously

^c Two fish had been recaptured previously

Mark-recapture study

Due to the small body size of *P. caprodes* (<10 cm length), the displacement of individuals was examined with a mark-recapture study rather than through telemetry techniques. In order to obtain reliable displacement estimates, the analytical framework developed by Rodriguez (2002) was used, where fish were marked and recaptured within a central “home” section, and in several recapture sections up- and downstream of the home section. This makes it possible to distinguish between potentially high turnover rates (i.e., a high proportion of individuals that moved outside a section over the study period) and displacement (i.e., a change in location such as from one section to the adjacent section), which could be low if individuals do not move far.

Fish were captured using backpack electrofisher (LR-24 Smith-Root, Inc., Vancouver, WA, USA), since other methods such as seining resulted in an extremely low number of fish and high turbidity precluded visual detection and capture in dip nets. Fish were marked with visible implant elastomer (VIE, Northwest Marine Technology, Inc., Shaw Island, WA, USA) in three 15 m long × 15–25 m wide home sections. Unfortunately, block nets, used to increase sampling efficiency, could not be placed successfully due to the high currents in the reach. Fish were recaptured in the home sections, and in three recapture sections (each 15 m long × 15–25 m wide) up- and downstream of the home sections. Marking occurred on four sampling days (separated by 10–17 days, Table 1) between the end of August and early October, 2007. To increase recapture rates (i.e., #individuals recaptured/# individuals marked), fish were also marked in the recapture sections on 4 October, 2 weeks before the last sampling date (18 October 2007).

Whereas we do not have direct evidence that *E. triquetra* releases its glochidia at this time in the Sydenham River, there are several lines of indirect evidence, from ongoing research in our laboratory, which suggest this is the case. Namely: (1) Gravid *E. triquetra* with viable glochidia were found a few km downstream of the study site between early August and early October, 2007 (K. McNichols, University of Guelph, pers. comm.); (2) surveys conducted between 2005 and 2009 and beginning in late May/early June, indicate that *E. triquetra* were first observed in a gravid state in the Sydenham River beginning in late July/early August (McNichols and Ackerman, unpublished); (3) Glochidia obtained from gravid females found in late summer/fall successfully transformed on *P. caprodes* in the laboratory with a relatively high transformation rate (McNichols 2007); and (4) A gravid *E. triquetra* released its glochidia immediately after we picked her up from the sediment in the fall (ANS, unpublished).

Mussels close their siphons in response to an electrical shock, but no effect on their survival has been reported (Holliman et al. 2007). The VIE used for marking fish was injected subcutaneously (posterodorsal and posteroventral), and provided clear, long-lasting marks with minimal fish mortality (Roberts and Angermeier 2004). Different coding (colors, location on the fish) was used to differentiate between sections and sampling dates. The distance moved by a fish between encounters (i.e., the displacement distance) was taken as the shortest distance between the centers of the sections in which the fish was caught (15 m between adjacent sections). This determination assumes that the mortality of *P. caprodes* after marking and recapture was negligible (i.e., all losses are due to emigration), and that the movements and recapture rates of *P. caprodes* did not vary temporally or spatially.

Statistical analysis-field study

A χ^2 test was used to determine whether there were differences in the number of fish that moved upstream versus downstream. ANOVA was used to determine whether displacement distances differed significantly among fish that were recaptured after 1–2, 2–3, 3–4, and >4 weeks. Assumptions of homogeneity of variances were examined using a Cochran test. The percentage of recaptures were ln-transformed ($\ln + 1$) and linear regression was used to determine whether recapture decreased exponentially with distance from the marking section. The turnover rate (i.e., the proportion of individuals that moved out of home section over the study period) was calculated according to Rodriguez (2002) as

$$\text{Turnover rate} = e^{-\lambda H} \quad (1)$$

where $\lambda = 1/\text{mean displacement distance}$, and $H = \text{home section length (15 m)}$.

Review of movement studies of small benthic fish

As indicated above, the vast majority of host fish that have been reported for *Epioblasma* species are darters and sculpins (Cummings and Watters 2005). Consequently, we consulted FishMaP (Fish Migration and Passage Knowledgebase, McLaughlin 2008), which includes fish movement and migration data, and the ISI Web of Knowledge for articles with quantitative movement data (displacement distances) on darters (Percidae: *Pecina* and *Etheostoma*) and sculpins (Cottidae: *Cottus*) (Table 4). Data on average and maximum displacement distances were gathered, but in several cases average displacement distances were based on displacement distance frequency distributions, and in one case, the home range size was used as a measure for average displacement distance (see

Table 4). We also collected information on study duration and spatial extent (as longitudinal distance), and recapture rates. We used the mean values for each species when more than one reference was available to avoid pseudoreplication, and differentiated between sculpins and darters because differences in morphology and life history between these taxa (e.g., elongate, terete, and somewhat laterally compressed with more mid-water depth behavior vs. spiny large-headed with broad mouths and somewhat dorsally compressed with demersal behavior, respectively; Scott and Crossman 1973) may affect their movement abilities. Data on displacement distances, spatial extent of the study, and the duration of the study were log-transformed to meet normality criteria of the test statistics. Analysis of Covariance (ANCOVA) was used to determine whether there were differences in the relationship between study design parameters (spatial extent of the study, study duration and recapture rate) and the maximum displacement distances for darters and sculpins.

Results

Field study

The overall recapture rate of *P. caprodes* was 16% ($n = 28$ of 175 marked fish, newly captured before 18 Oct 2007), and three of these individuals were recaptured twice (Table 1). The majority of all recaptures (82%) occurred within 30 m of their original capture location (i.e., 15 m up or downstream, Fig. 1), with a mean displacement distance of 13 ± 3 m [mean \pm standard error (SE), $n = 28$] and a range of 0–75 m. The mean displacement distance for fish marked in home sections was similar at 17 ± 5 m ($n = 17$; grey bars in Fig. 1).

Most of the recaptures ($n = 21$) occurred after ~ 2 weeks (10–17 days), with a range of 1.4–5.4 weeks (Table 1, Fig. 2). The highest displacement rate, however, was found for recaptures after less than 2 weeks (10 ± 5 m/week, $n = 7$; Fig. 2). There was a slight decrease of displacement rate with increasing time between mark and recapture, however, this was not statistically significant ($F_{2,1} = 0.7, p = 0.5$; Fig. 2). Mean displacement distances for *P. caprodes* did not change significantly over the study period (Table 1).

There was no significant difference between up- and downstream displacement distances ($X^2_1 = 0.06, p = 0.999$, Fig. 1), therefore up- and downstream data were pooled for further analysis. The percentage of *P. caprodes* recaptures decreased exponentially with distance from the marking section ($R^2 = 0.83, p < 0.01$, Fig. 3). Extrapolation of the regression results showed that 1 in 100 recaptures would be found at 76 m (95% prediction interval: 28–137 m). The estimate for the turnover rate, i.e., the

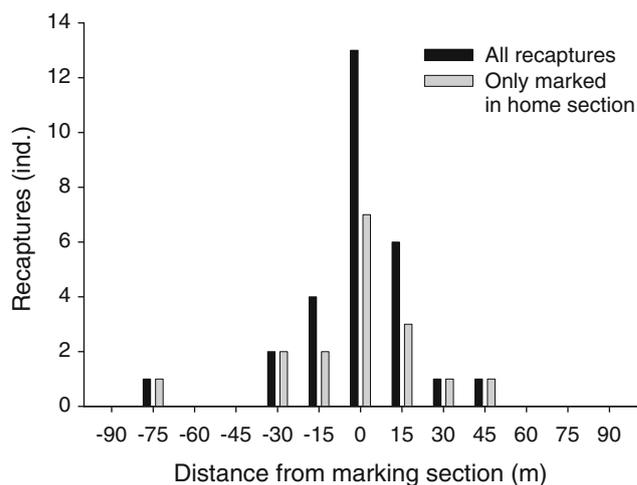


Fig. 1 Number of *Percina caprodes* recaptures and the distance from marking section. Negative numbers indicate downstream distance

proportion of individuals that moved out of a home section over the study period, ranged between 0.3 (for $1/\lambda = 13$ m, all recaptures) and 0.4 (for $1/\lambda = 17$ m recaptures for fish marked in home section) and did not vary much between sampling dates (Table 1). The estimates were 0.18/month and 0.24/month when the data were normalized by the study duration and they declined with time (Table 1).

Review of movement studies of small benthic fish

Data for five sculpin (*Cottus bairdi*, *C. cognatus*, *C. gobio*, *C. pollux*, and *C. rhenanus*) and nine darter species (*Etheostoma flabellare*, *E. nigrum*, *E. podostemone*, *E. spectabile*, *Percina caprodes*, *P. evides*, *P. nigrofasciata*, *P. rex*, and *P. roanoka*) were included in the analysis (i.e., $n = 14$ species; Table 4). Average displacement distances

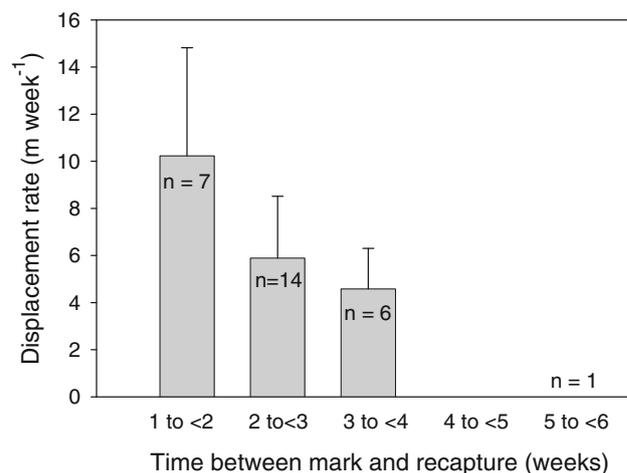


Fig. 2 Absolute displacement of recaptured *Percina caprodes* in relation to the time between marking and recapture. The error bars represent SE

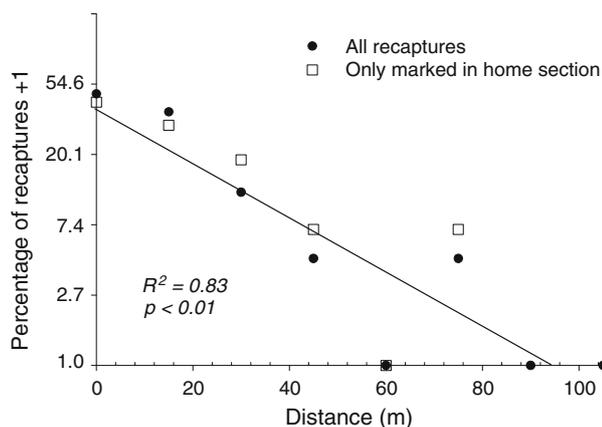


Fig. 3 The relationship between the percentage of *Percina caprodes* recaptures (*ln scale*) and the distance away from the marking section (up- and downstream combined). The regression line is based on all recaptures [$\ln(\text{recaptures} + 1) = (-0.039 \pm 0.007)(\text{estimate} \pm \text{SE})\text{distance} + 3.68 \pm 0.46]$, $R^2 = 0.83$, $p < 0.01$

were higher for darters (45 ± 29 m, $n = 9$) compared to sculpins (23 ± 9 m, $n = 5$) as were the spatial extent examined ($2,854 \pm 2,519$ m vs. 389 ± 52 m, respectively; Table 2). This was due in part to the inclusion of *P. rex*, which had an unusually large mean displacement distance of 275 m in a study that extended over 23 km (Table 4). The pooled data revealed a mean displacement distance of 37 ± 19 m and a maximum displacement distance of 462 ± 214 m (Table 2).

ANCOVA revealed that there was a positive significant relationship between the spatial extent of the study and the maximum displacement distance (ANCOVA $R^2 = 0.83$, $F_{2,11} = 32.1$, $p < 0.001$, Fig. 4a, Table 3), which remained evident when the *P. rex* data (largest spatial extent = 23 km) were removed [ANCOVA $R^2 = 0.69$, $F_{2,10} = 14.2$, $p = 0.001$; R^2 presented in Fig. 4 are derived from linear regression, and do not include fish group (darters vs. sculpins) as a covariate as per the ANCOVA R^2]. In this case, no differences were detected between darters and sculpins ($p = 0.84$, Table 3). A significant positive relationship was also found between the duration of the study and the maximum displacement distance (ANCOVA $R^2 = 0.72$, $F_{2,11} = 17.5$, $p < 0.001$) including differences between darter and sculpins ($p = 0.01$, Fig. 4b,

Table 3). However, this relationship was less evident when the *P. rex* data (study with the longest study duration of 96 months) were removed (ANCOVA $R^2 = 0.37$, $F_{2,10} = 7.6$, $p = 0.04$). Not surprisingly, there was a strong correlation between the spatial extent and the study duration ($r = 0.76$, $p = 0.001$). No relationship was detected between recapture rate and the maximum displacement distance (ANCOVA $R^2 < 0.01$, $p = 0.41$, Fig. 4c, Table 3). Interestingly, similar findings were also found using data grouped by study rather than by species (data not provided).

Discussion

This study takes a first step towards understanding the dispersal abilities of *E. triquetra* via the movement behavior of its obligate host fish, *P. caprodes*. We found that the movement of *P. caprodes* was limited to a few to tens of meters. However, a small proportion moved greater distances (max. 75 m), and the percentage of recaptures decreased exponentially with distance. Extrapolation of these results revealed that few individuals would move ~ 100 m, and perhaps greater distances, if the distribution of movements was leptokurtic (Petty and Grossman 2004). It is important to note that the displacement rates did not increase with increasing time between mark and recapture even though the turnover rate, i.e., the proportion of individuals that moved outside a section over the study period, was relatively high (i.e., 0.3–0.4). However, high turnover rates do not necessarily indicate high displacement rates given that the variation in turnover rates in stream salmonids (0.15–0.7) appeared to be unrelated to displacement distances in a recent review (Rodriguez 2002).

The low average displacement distance of *P. caprodes* measured in this study is consistent with the average displacement distances reported for other small benthic fish (Table 2). The maximum displacement distance is also consistent with these studies but falls at the lower part of the range of the maximum distances presented in Fig. 4. This is because the maximum displacement distance is dependent on both the spatial extent and the duration of the

Table 2 Summary of reported movement data and recapture rate, study duration, spatial extent of movement studies of darters and sculpins

	Average distance (m)	Maximum distance (m)	Recapture rate (%)	Study duration (months)	Spatial extent (m)
Sculpins ($n = 5$)	23 ± 9 (4–50)	258 ± 47 (174–435)	42 ± 6 (21–52)	13 ± 3 (7–24)	389 ± 52 (300–565)
Darters ($n = 9$)	45 ± 29 (11–275)	567 ± 333 (58–3,200)	23 ± 6 (5–66)	14 ± 10 (1–96)	$2,854 \pm 2,519$ (100–23,000)
Pooled ($n = 14$)	37 ± 19 (4–275)	462 ± 214 (58–3,200)	30 ± 5 (5–66)	14 ± 7 (1–96)	$1,973 \pm 1,618$ (100–23,000)

Values presented are the mean \pm SE, and the range in parenthesis. The sample size (n) refers to the number of species

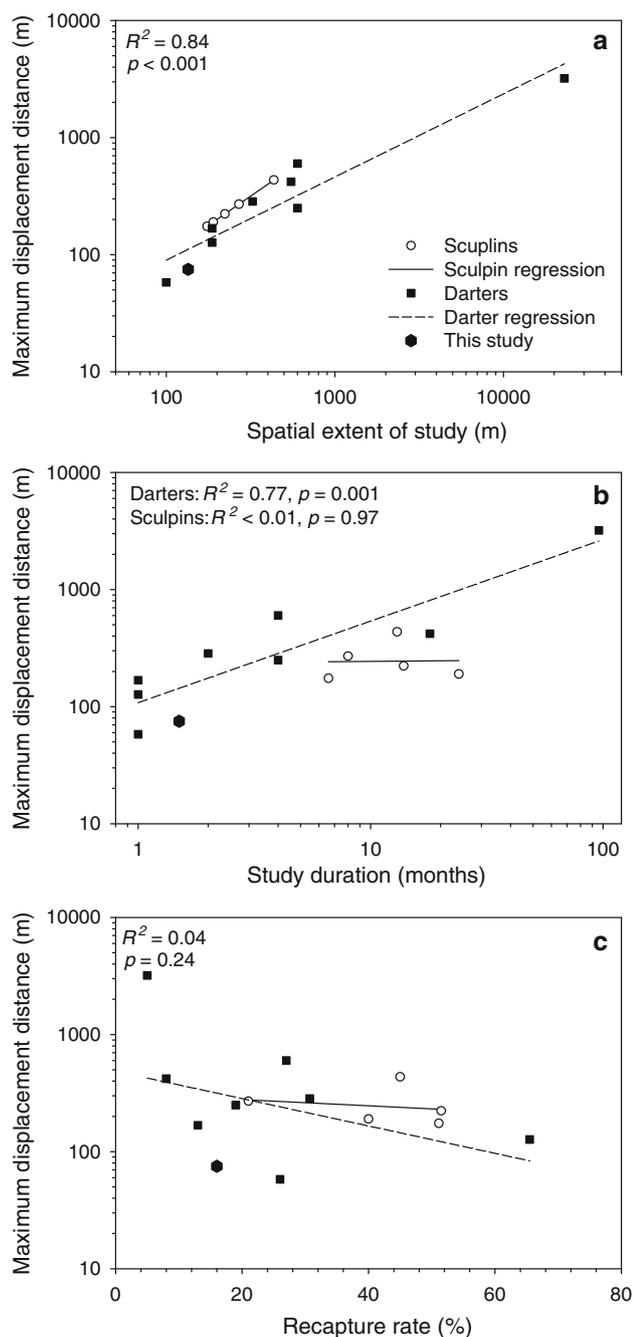


Fig. 4 The maximum displacement distances in movement studies of sculpins and darters in relation to the **a** spatial extent of the study, **b** the study duration, and **c** the recapture rate. Each dot represents one species (see also Table 4). The regression lines are provided for darter and sculpin species. R^2 from linear regressions are based on pooled results except when significant differences were detected between darter and sculpin species under ANCOVA (ANCOVA R^2 reported in Table 3)

study (see Fig. 4). Hence, it is likely that we would have observed larger maximum displacement distances for *P. caprodes* if our study was extended over a larger spatial area for a longer period of time.

In addition to the limited spatial extent of this study, we cannot rule out the possibility that fish moved larger distances, since our recapture rate was relatively low. However, our recapture rate was consistent with those of the small benthic fish reviewed in Table 2 and the recapture rates of other small benthic fish (e.g., Freeman 1995; Labbe and Fausch 2000; Roberts and Angermeier 2007). They are low relative to other studies (Schaefer et al. 2003; Petty and Grossman 2004; McLain and Ross 2005) in which fish were observed visually and, in two of the three studies, caught in dip nets.

This study was undertaken between August and early October, 2007, which includes *E. triquetra*'s gravid period (McNichols and Ackerman unpublished). Given that glochidia are expected to be encysted (or encapsulated) on fish for a couple of weeks (McNichols 2007), it is reasonable to suggest that offspring of *E. triquetra* will have limited dispersal via movement of *P. caprodes* in the Sydenham River, unless colder temperatures prolong encystment. Larger dispersal of *E. triquetra* via *P. caprodes* could occur if glochidia are attached during a time when the fish are more mobile such as during periods of high discharge (Petty and Grossman 2004) that occur in late winter/early spring. However, it is not known whether glochidia of *E. triquetra* overwinter on its host fish, which has been suggested for other unionid species like *Lampsilis cardium* (Watters and O'Dee 1999), nor whether *E. triquetra* also releases glochidia during host capture early in the spring when high water levels impede mussel surveys in the Sydenham River. Upstream bias of movements as observed during breeding in other smaller fish (Lamphere 2005) could occur in late spring during *P. caprodes* spawning season. This may occur in rivers like the Clinton River, Michigan, where *E. triquetra* glochidia have been found in the water column between mid May to mid July (Sherman 1994), but it should also be noted that the timing of the glochidia release is likely temperature dependent (Watters and O'Dee 2000).

It was generally held that darters and sculpins either do not migrate or undertook small migratory movements (e.g., spawning movements) often <100 m (Lucas and Baras 2001). However, it is evident from our review that a small fraction of the population may move considerable distances, whereas the majority move relatively little (Neely and George 2006; Breen et al. 2009). The reasons behind this mixed strategy within a population remains to be determined, but for mussels that rely on smaller benthic fish as hosts, the restricted movement of the majority of the host fish population may ensure that most of their offspring remain in the same optimal habitat and that the local mussel population persists. The larger movement of a small fraction of the host fish population, on the other hand, may be important to colonize new habitat and to avoid

Table 3 Results from the ANCOVA analyses that examined whether there were differences in the relationship between the predictor variable (e.g., study design parameters: spatial extent of the study, study duration and recapture rate) and the maximum displacement distances for darters and sculpins

Coefficients			ANCOVA		
Predictor	<i>p</i> Value for predictor	<i>p</i> Value for differences among fish groups	<i>R</i> ²	<i>F</i> _{2,11} -value	<i>p</i> Value
Spatial extent of study	<0.001	0.84	0.83	32.1	<0.001
Study duration	0.78	0.01	0.72	17.5	<0.001
Recapture rate	0.87	0.49	<0.01	0.98	0.41

Regression results are presented in Fig. 4

detrimental effects of a closed population such as genetic inbreeding.

It is clear that further study of the dispersal abilities of *E. triquetra* and other unionid species are needed. Rare and less mobile species will likely recover more slowly after local extinctions (Albanese et al. 2009). Thus limited dispersal via small benthic host fish may provide an indication of extinction risk via habitat fragmentation (Strayer 2008). This may be the case for *E. triquetra* in the Sydenham River where known populations at survey sites are several km apart. Unfortunately little data is available on their distribution between survey sites. Thus, the connectivity between mussel patches may be low even if a few fish move larger distances. The limited potential for colonization from other populations (the ‘rescue effect’, Hanski 1999) may help

to explain why *E. triquetra* and other *Epioblasma* species are highly imperiled (Nature Serve 2009).

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Appendix

See Table 4.

Table 4 Summary of movement data of darters and sculpins

Species	Capture method	Section lengths (m)	Spatial extent (m)	Study duration (months)	Recapture rate (%)	Mean (median) distance (m)	Max. distance (m)	Study
<i>Cottus bairdi</i>	Pit-tagging	10	700	12	76 (detection efficiency)	7 (4)	511	Breen et al. (2009)
	Electrofishing	20	200	24	23	23 (5)	160	Lamphere (2005)
	Hand-netting	<0.5	200	1.5	79	4 (1.3)	165	Petty and Grossman (2004)
	Hand-netting	3–27	177	18	28	13 ^b	55	Hill and Grossman (1987)
Average ± SE (range)			319 ± 127 (177–700)	14 ± 5 (1.5–24)	52 ± 15 (23–79)	12 ± 4 (4–23)	223 ± 99 (55–511)	
<i>Cottus cognatus</i>	Electrofishing	10	140	10	44	(9)	101	Cunjak et al. (2005)
	Weir traps	>14	1,600	1	30	(26)	209	Schmetterling and Adams (2004)
Average (range)			870	6	37	18	155	
<i>Cottus gobio</i>	Electrofishing	10	310	8	21	38	270	Knaepkens et al. (2005)
<i>Cottus pollux</i>	Hand-netting	2	300	24	40	(4)	192	Natsumeda (2007)
<i>Cottus rhenanus</i>	Electrofishing	5	450	13	45	50	435	Ovidio et al. (2009)

Table 4 continued

Species	Capture method	Section lengths (m)	Spatial extent (m)	Study duration (months)	Recapture rate (%)	Mean (median) distance (m)	Max. distance (m)	Study
<i>Cottus</i> Average \pm SE (range) $n = 5$			389 \pm 52 (300–565)	13 \pm 3 (7–24)	42 \pm 6 (21–52)	23 \pm 9 (4–50)	258 \pm 47 (174–435)	
<i>Etheostoma flabellare</i>	Seining	>10	187	1	39	8 ^a	185	Mundahl and Ingersoll (1983)
	Seining	>8	187	1	40	14 ^a	168	Ingersoll et al. (1984)
	Electrofishing	47 \pm 25 (mean \pm SD)	600	4	13	10 ^a	500	Roberts and Angermeier (2007)
Average \pm SE (range)			325 \pm 138 (187–600)	2 \pm 1 (1–4)	31 \pm 9 (13–40)	11 \pm 2 (8–14)	284 \pm 108 (168–500)	
<i>Etheostoma nigrum</i>	Seining	>10	187	1	91	2 ^a	109	Mundahl and Ingersoll (1983)
	Seining	>8	187	1	40	19 ^a	145	Ingersoll et al. (1984)
Average (range)			187	1	66	11	127	
<i>Etheostoma podostemone</i>	Electrofishing	47 \pm 25 (mean \pm SD)	600	4	19	11 ^a	250	Roberts and Angermeier (2007)
<i>Etheostoma spectabile</i>	Seining	>8	187	1	13	26 ^a	168	Ingersoll et al. (1984)
<i>Percina caprodes</i>	Electrofishing	15	135	1.5	16	13	75	This study
<i>Percina evides</i>	Hand-netting	<0.5	100	1	26	11 ^a	58	Skyfield and Grossman (2008)
<i>Percina nigrofasciata</i>	Wire traps	18–33	550	18	8	37 ^a	420	Freeman (1995)
<i>Percina rex</i>	Electrofishing	55–160 m	23,000	1998–2006	5	275 ^a	3,200	Roberts et al. (2008)
<i>Percina roanoka</i>	Electrofishing	47 \pm 25 (mean \pm SD)	600	4	27	12 ^a	600	Roberts and Angermeier (2007)
<i>Etheostoma</i> and <i>Percina</i> Average \pm SE, $n = 9$ (range)			2,854 \pm 2,519 (100–23,000)	14 \pm 10 (1–96)	23 \pm 6 (5–66)	45 \pm 29 (11–275)	576 \pm 333 (58–3,200)	
Overall Average \pm SE (range), $n = 14$			1,973 \pm 1,618 (100–23,000)	14 \pm 7 (1–96)	30 \pm 5 (5–66)	37 \pm 19 (4–275)	462 \pm 214 (58–3,200)	

Recapture rate = individuals recaptured/marked. Standard errors (SE) were not calculated when $n < 3$

^a Mean estimated from frequency data (Histograms of frequency vs. distances)

^b Based on home range estimates (cited in papers)

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