

# Limited movement of freshwater mussel fish hosts in a southern US river

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**Abstract** Organisms that live in flowing water need to compensate for downstream displacement. Mobile animals can compensate for displacement by actively swimming or crawling upstream, while sedentary animals need other means to retain their position. Freshwater mussels (*Bivalvia*, *Unionidae*) have limited movement as adults, and juveniles drift downstream after excystment from their host. Mussel larvae are ectoparasites on fish, and it has been assumed that fish move larvae back upstream; however, this has not been tested experimentally. We hypothesized that fish served as dispersal agents, and that fish movement had an upstream bias to compensate for displacement of mussels by drift. We conducted a mark-and-recapture study of host fish in four 100-m reaches of the Little River, OK, USA, in the summer of 2011. Our study

took place during a drought, and overall captures decreased with decreasing discharge, likely because fish moved out of their home ranges into deeper pools. Most recaptured fishes were centrarchids, and most recaptures occurred within 20 m of initial capture transects. While most moved <20 m, when fish did move to longer distances, they moved more upstream than downstream, allowing mussels to compensate for displacement.

**Keywords** Upstream compensatory movement · Downstream drift dispersal · Turbulent flow · Patchiness · Juvenile unionid mussels · Host fish species

## Introduction

Organisms that live in flowing water need to resist or compensate for downstream displacement during high flows and associated turbulent conditions (Elliott, 1971). Larger and more mobile animals such as fish can compensate for downstream displacement by moving back upstream, while smaller and less mobile animals such as many aquatic invertebrates must use other means to compensate for their displacement. Some aquatic insects have a winged adult stage that includes pre-oviposition, upstream flight (Wilzbach & Cummins, 1989; Anholt, 1995; Koop et al., 2001). Other examples for compensatory movement include

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the upstream crawling of insect larvae and nymphs on the substrate or in the interstitial space of the hyporheic zone (Brittain & Eikeland, 1988), upstream swimming of amphipods (Elliott, 1971; Townsend & Hildrew, 1976; Williams & Williams, 1993), and the directed upstream movement of pulmonate aquatic snails (Kappes & Haase, 2012).

Freshwater mussels (Bivalvia, Unionidae; hereafter “mussels”) are sedentary organisms with adult movement ranges generally limited to several meters (Schwalb & Pusch, 2007; Allen & Vaughn, 2009; Gough et al., 2012). Mussels often occur in dense, multi-species aggregates known as mussel beds that are patchily distributed in areas of a river with stable sediments and low shear stress (Allen & Vaughn, 2009; Haag, 2012). Mussels that have been dislodged after substrate scouring during floods can be washed downstream, potentially into less suitable habitat (Strayer, 1999). Juvenile mussels are also subject to drift displacement (Schwalb et al., 2010; Irmscher, 2014). Since mussels have limited movement, repeated dislodgement and cumulative displacement should result in mussel beds being moved downstream over extended time periods (Layzer & Madison, 1995). However, mussel beds are generally not displaced over ecological time scales. In fact, we documented mussel beds that have been in the same location for over 100 years (Vaughn, 2000). This is likely due to the fact that mussels have a facet of their life history that allows them to compensate for downstream displacement.

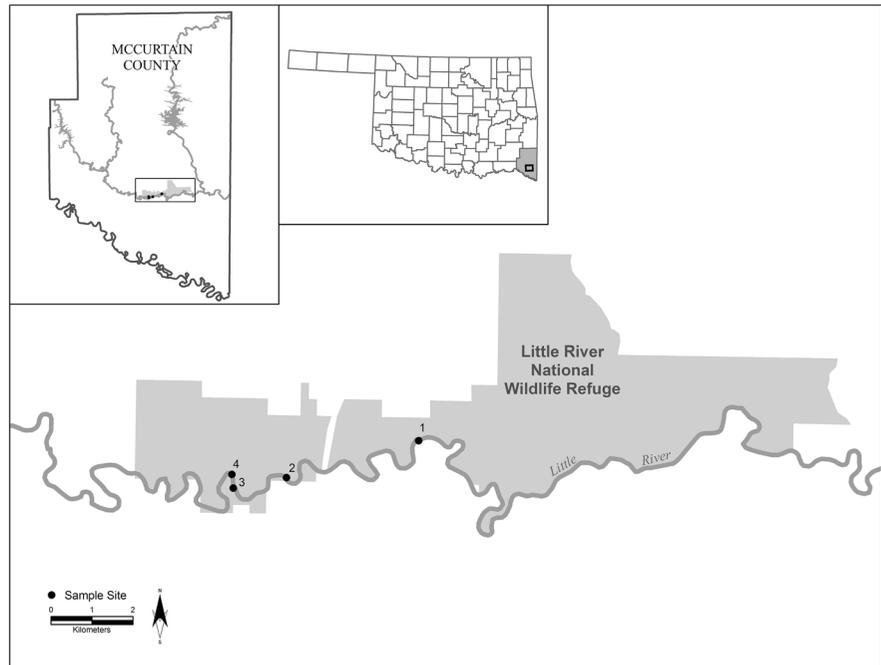
Mussels have a larval stage, glochidia, that are obligate ectoparasites on the fins and gills of fish (Barnhart et al., 2008; Haag, 2012). Glochidia metamorphose into juveniles that excyst from the host and sink to the bottom where they grow into adults. It has been long assumed that fish hosts serve as dispersal agents for otherwise sedentary mussels by moving glochidia back upstream (Watters, 1992; Strayer, 2008; Haag, 2012). Genetic evidence supports this assumption (Berg et al., 1998). However, the importance of fish as dispersal agents has rarely been tested experimentally. We examined this hypothesis with a mark-and-recapture study of the movement of host fish at four mussel beds during the mussels’ peak reproductive time period. We predicted an overall upstream movement trend of host fish, counteracting the downstream displacement of adult and juvenile mussels over time.

## Methods

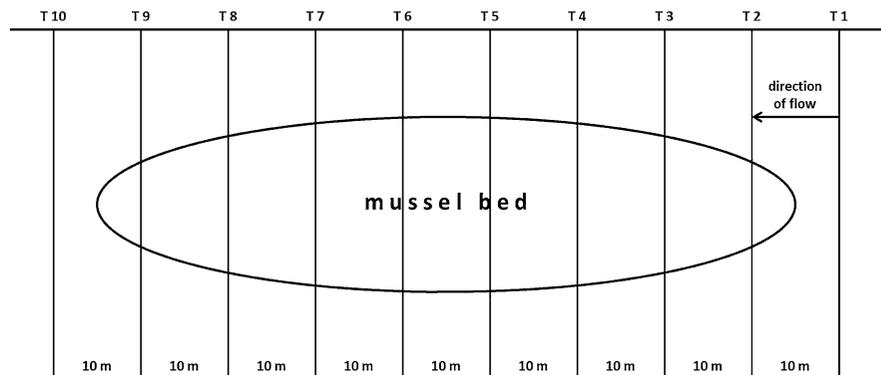
We conducted our study in the Little River in southeastern Oklahoma, USA. This well-studied river (watershed area 10,720 km<sup>2</sup>) has ~110 fish and ~38 mussel species, three of them endangered (Vaughn & Taylor, 1999; Matthews et al., 2005; Galbraith et al., 2008). Study sites were 100-m reaches, each containing a large mussel bed. All sites were located on a USFWS wildlife refuge (Fig. 1). We conducted our study in June through August 2011, which is the peak reproductive time for many of the local mussel species. Based on the well-known mussel fauna of this river (Appendix S1—Supplementary Material), we combined information from published literature and a continuously updated mussel–fish host database to identify host fishes for mussel species at these four sites (Appendix S2—Supplementary Material). The most important host fish groups in the Little River are sunfish and bass (Centrarchidae), catfish (Ictaluridae), gar (Lepisosteidae), freshwater drum (Sciaenidae), golden redhorse (Catostomidae), darters (Percidae), and shiners (Cyprinidae).

At each site, we used wading and snorkeling (with SCUBA in deeper areas) to identify the upstream and downstream extent of the mussel bed and established ten transects that were spaced 10 m apart, the first being the most upstream transect (Fig. 2). We sampled the fish communities within each 100-m site weekly with a backpack electro-fisher (Smith & Root, Model 12-A), traversing each transect twice (Büttiker, 1992; Schlosser, 1995; Smithson & Johnston, 1999). We chose electro-fishing as a collection method because it has been used frequently and effectively (Bohlin et al., 1989; Schlosser, 1995; Lucas & Baras, 2000), and because abundant underwater obstacles prevented the use of seines. At each transect, we placed captured individuals in a plastic bucket and marked those from host fish species by dorsal fin ray clipping and/or subdermal injection of acrylic dyes (Freeman, 1995; Lucas & Baras, 2000; Catalano et al., 2001). The marks indicated the transect of initial capture for each individual. We selected these marking techniques because they are inexpensive and easy to perform (Mourning et al., 1994; Freeman, 1995; Lucas & Baras, 2000), they were suited for the length of our study (Zerrenner et al., 1997), and they did not have negative effects on fish health and performance (Hughes et al., 2000). We treated fish with API Stress

**Fig. 1** Location of the Little River and sample sites in McCurtain County, OK. The USGS Lukfata Creek gage (discharge data) is located between Sample Sites 1 and 2, the HOB0<sup>®</sup> logger (water depth data) was placed at Site 1. All sample sites are located on the USFWS Little River National Wildlife Refuge ([http://www.fws.gov/refuge/little\\_river/](http://www.fws.gov/refuge/little_river/))



**Fig. 2** Schematic of transect sampling in river reaches. The diagram shows the alignment of transects in 10-m increments over mussel beds with the first transect being the most upstream



Coat Fish Conditioner (API Mars Fishcare, Chalfont, PA) and released them at the initial capture transect. In subsequent weeks, newly captured and recaptured individuals were marked using the same techniques. Dorsal fin ray clipping and dye color coding allowed us to determine the distance an individual had moved in relation to its transect of initial capture. Unfortunately, small fish (darters, shiners) showed high sensitivity to capturing and marking, and high mortality rates forced us to omit them from our study early on.

We quantified fish movement using histograms, with downstream moves assigned negative values and upstream moves assigned positive values. Then, to

assess any directional bias, we tested for kurtosis and skewness in the distribution of fish movement (Sokal & Rohlf, 1997; Lowe, 2003).

We obtained discharge data from the USGS Little River Lukfata Creek gage near Idabel, OK. The gage is located between Sites 1 and 2 (Fig. 1). In addition, we continuously recorded water depth at Site 1 with a HOB0<sup>®</sup> data logger (Onset Computer Corporation, Cape Cod, MA). We used linear regression to examine the relationship between fish movement and flow and depth. Statistical analyses were performed with IBM SPSS Statistics, Version 19 (IBM Company, Armonk, NY).

## Results

We captured 765, and recaptured 89 (11.63%) fish, most of them at the transect of initial capture (Table 1; Fig. 3). Movement was highly leptokurtic ( $g_2 = 8.622 \pm 1.279$ ,  $P < 0.001$ ) and significantly right-skewed ( $g_1 = 2.879 \pm 0.661$ ,  $P < 0.001$ ), indicating that most fish were basically stationary during our study, but those that did move tended to move upstream (Fig. 3). Recaptures decreased with increasing distance from original capture transects in either direction. On average, recaptured individuals moved 2.25 ( $\pm 14.04$  SD) m upstream. This trend of little to no movement was observed for all fish groups investigated, and most recaptures occurred within 20-m upstream or downstream of the initial capture transect (Fig. 3).

Centrarchids comprised the largest proportion of all recaptures (Fig. 4). Although sunfish movement ranged from 30 m downstream to 50 m upstream, most individuals remained in their initial capture transect. Mean movement was 3.38 ( $\pm 13.37$  SD) m upstream

(Fig. 4). Bass had a slightly larger movement range of 50 m down- to 20-m upstream, while recaptures for other fish groups were low (catfish, freshwater drum, golden redhorse) or did not occur at all (gar). When individuals were recaptured, this occurred in the transect of original capture (Fig. 4).

The mean number of fish captured decreased with a decrease in mean discharge over the course of our study period (Fig. 5). Coincidentally, an increase in discharge in the end of the study period was associated with a concurrent increase in mean fish captures. In addition, the number of fish captured at all sites was positively correlated with changes in water depth ( $R^2 = 0.74$ ,  $P = 0.027$ ) (Fig. 6).

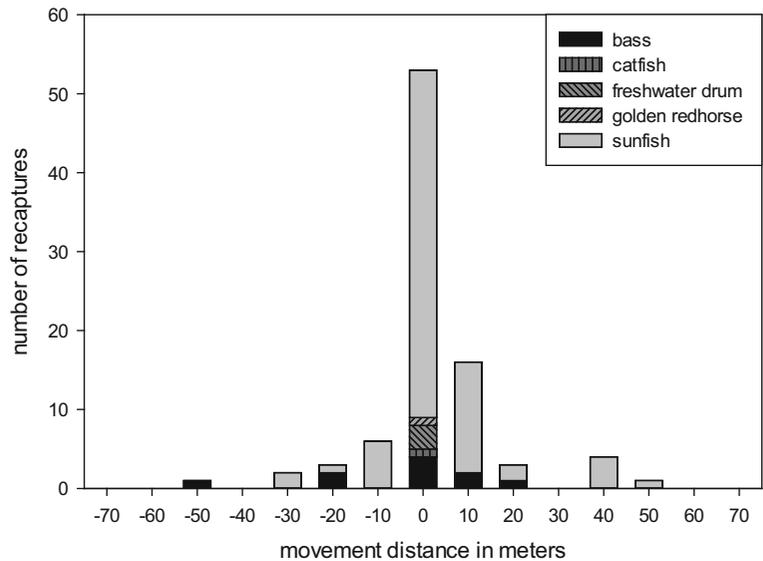
## Discussion

In our study of host fish movement, most fish moved less than 20 m. In addition, when fish moved, they showed a greater tendency to move upstream than

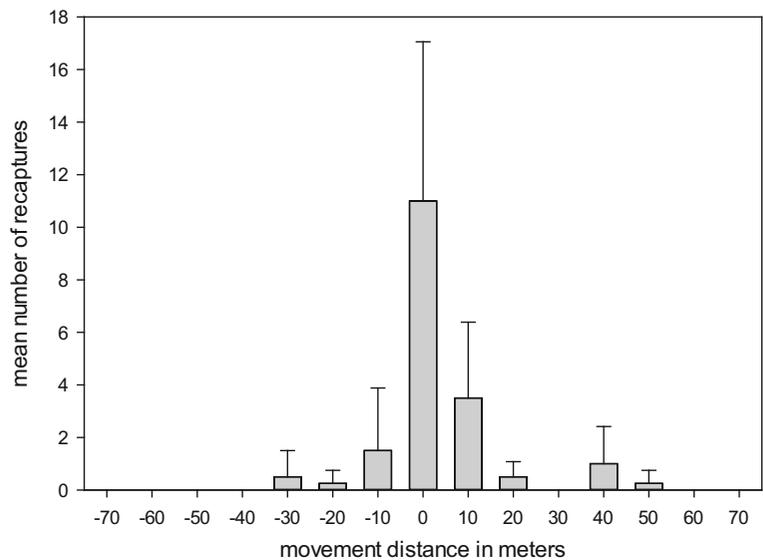
**Table 1** Number of fish captures and recaptures by site and date

Sample Site	Sample Date	Number of captures	Number of recaptures
Site 1	06/29/11	34	n/a
Site 1	07/05/11	52	12
Site 1	07/19/11	44	2
Site 1	07/24/11	11	3
Site 1	08/16/11	27	2
Site 1	08/24/11	23	3
Site 2	06/30/11	55	n/a
Site 2	07/06/11	51	3
Site 2	07/20/11	46	7
Site 2	07/25/11	39	14
Site 2	08/16/11	30	3
Site 2	08/24/11	6	1
Site 3	07/01/11	45	n/a
Site 3	07/07/11	30	2
Site 3	07/21/11	22	2
Site 3	07/26/11	27	2
Site 3	08/18/11	16	1
Site 3	08/25/11	12	0
Site 4	07/08/11	42	n/a
Site 4	07/22/11	60	10
Site 4	07/27/11	51	15
Site 4	08/18/11	32	3
Site 4	08/25/11	10	4

**Fig. 3** Number of fish recaptured per movement distance. *Bar graph* subsections represent the number of fish for each fish group at the respective distances from the original capture transect. *Negative numbers* represent distances moved downstream of the initial capture transect, positive numbers movement distances upstream



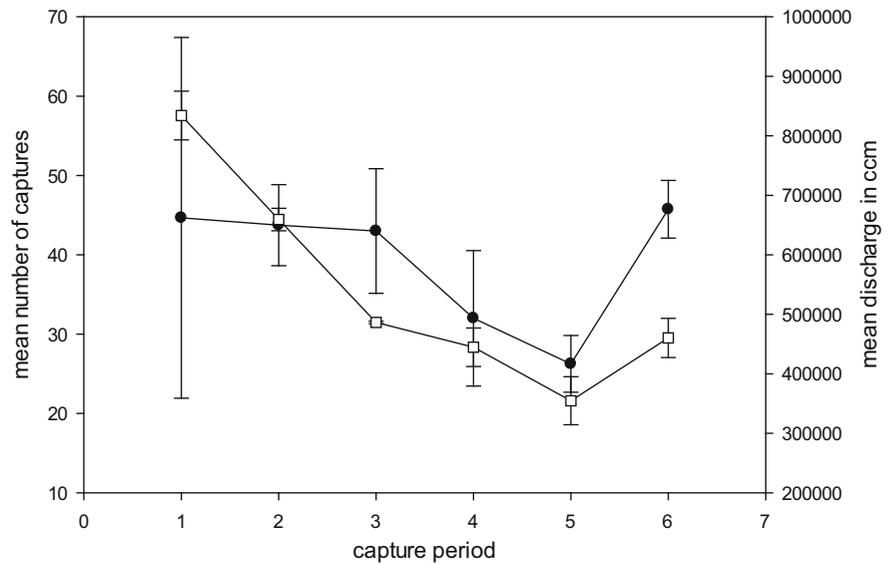
**Fig. 4** Mean number of centrarchids recaptured in relation to movement distance. *Error bars* represent standard deviations



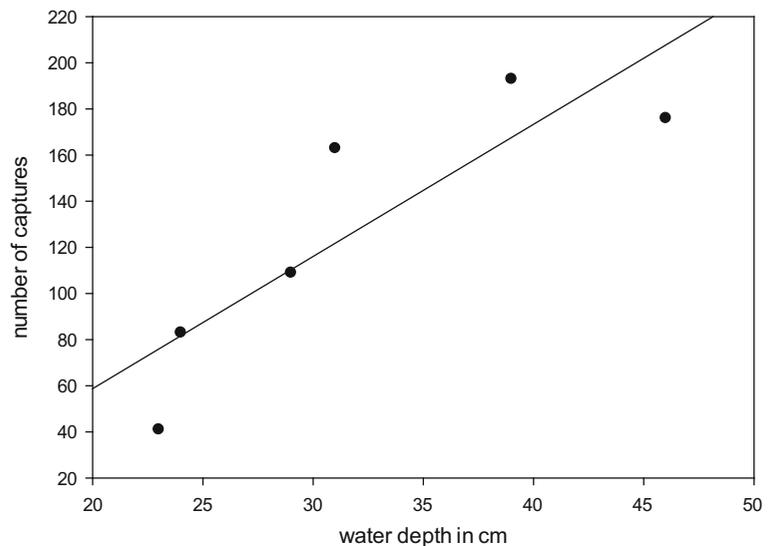
downstream. The potential upstream movement of mussel glochidia via fish hosts could compensate for downstream displacement of adults and juveniles, and help maintain mussel populations by enhancing local recruitment (Schwalb et al., 2011; Terui et al., 2014). Kopp et al. (2001) introduced the term Exact Compensation to describe net upstream movements of stream organisms that *exactly* compensate for the drift of propagules settling in the vicinity of the parents. The idea that upstream migration by immature stages of stream animals compensates for downstream drift

has been previously considered (e.g. Bishop & Hynes, 1969; Elliott, 1971; Bird & Hynes, 1981; Williams & Moore, 1982; in Wilzbach & Cummins, 1989), but has not been experimentally examined in mussels. Based on previous studies investigating the sinking and drift rates of juvenile mussels (Schwalb et al., 2010; Schwalb & Ackerman, 2011; Irmscher, 2014), we estimated that juveniles drift approximately 50–250 cm during summer low flow conditions in the Little River, which is within the same range of upstream movement of host fish that we measured.

**Fig. 5** Mean number of captures in relation to discharge over time. Mean discharge in the Little River (white boxes) and mean number of fish individuals captured (black circles) over the duration of the study (capture periods). Error bars represent standard errors



**Fig. 6** Number of captures (original captures + recaptures) in relation to water depth



Studies of mussel–host relationships have frequently investigated luring strategies and other aspects of glochidia–host interactions that enhance recruitment (e.g., Sietman et al., 2012); however, upstream dispersal is an additional advantage that mussels gain from the relationship with their host (Mansur & da Silva, 1999; Barnhart et al., 2008; Horký et al., 2014).

Our study of host fishes at four sites in one season is a snapshot in time and space. However, many stream fishes have been shown to have a tendency to move upstream in the summer (Gatz & Adams, 1994).

Centrarchids are common and frequently used hosts of unionid mussels (Haag & Warren, 1997; Khym & Layzer, 2000) and have a greater tendency to move up-rather than downstream (Freeman, 1995). The same is true for white crappie (*Pomoxis annularis*), small-mouth bass (*Micropterus dolomieu*), and yellow bullhead (*Ameiurus natalis*) (Funk, 1957). Upstream movements in mottled sculpins (*Cottus bairdii*) were 23.4% greater than downstream (McCleave, 1964), and both the common carp (*Cyprinus carpio*) and gizzard shad (*Dorosoma cepedianum*) move upstream

in large numbers (Winston et al., 1991). A study by Gerking (1950) showed that stream fish moved upstream an average of 33.5 m farther than downstream during high flows. This makes sense since not only adult fish but also propagules are subject to currents that move eggs and fry downstream (Larimore et al., 1959; Platania & Altenbach, 1998; Zitek, 2006). Upstream movement is often tied to reproduction and necessary for gene dispersal, and to maintain local populations (Hall, 1972).

Although fish that moved tended to move upstream, most fish in our study had short or no movements from their initial capture location. Many stream fish can be considered sedentary, spending their entire lives within just one pool or a reach, their home range (Gerking, 1959; Gatz & Adams, 1994; Freeman, 1995; Petty & Grossman, 2004). For example, sunfishes tend to have restricted movement (Smithson & Johnston, 1999; Paukert et al., 2004), and Gerking (1953) showed that sunfish occupied the same home range for two to possibly 3 years. Freeman (1995) found that 93% of juvenile centrarchids and 88% of darters were recaptured within 33 m of the initial capture location. Limited movement can be particularly prevalent during times of reproduction when many stream fish occupy territories that they defend aggressively against competitors (Gerking, 1953; Scalet, 1973; Bridcut & Giller, 1993). The reproductive behavior of sunfish that includes the building of breeding nests and aggressive defense against intrusion of predators and competitors is a prime example of this (Gatz & Adams, 1994).

Most home ranges of stream fishes are <100 m (Rodriguez, 2002), which is within the spatial extent of the mussel beds we studied. In combination with the low juvenile mussel drift distances that we documented in the Little River during summer low flow conditions (Irmscher, 2014), restricted movement of host fish during periods of peak glochidial infestation could contribute to the aggregated, patchy distribution of mussels (Brittain & Eikeland, 1988; Watters, 1992; McLain & Ross, 2005). If fish hosts do not move far, most mussel propagules will be deposited within the mussel bed leading to localized, positive feedbacks between mussel density, fish hosts, and mussel recruitment. Infestation of European chub (*Squalius cephalus*) with duck mussel (*Anodonta anatina*) glochidia resulted in a reduction of the host's activity and movement, restricting mussel dispersal (Horký

et al., 2014). Similar to our study, Terui et al. (2014) found an overall upstream bias in movements of Masu Salmon (*Oncorhynchus masou masou*), the host of the Japanese freshwater pearl mussel (*Margaritifera laevis*), recapturing ~70% of hosts near original capture locations. Schwalb et al. (2011) recaptured 82% of logperch (*Percina caprodes*) within 30 m of original capture locations, and McLain & Ross (2005) recaptured 94% of all marked tessellated darters (*Etheostoma olmstedi*) in those locations where they were originally marked. All these studies support our findings of limited movement of many fishes that are hosts to mussels.

It is important to keep in mind that there is variation in movements of stream fish within and between species (Funk, 1957). While most individuals move only little, some will move over intermediate, and a few over long distances (Wiens, 1976; Smithson & Johnston, 1999; Fausch et al., 2002). Movements over long distances occur in juvenile fish and less competitive individuals (Fish & Savitz, 1983; Freeman, 1995) and are also necessary to recolonize previously defaunated stream sections (Gatz & Adams, 1994). Some life histories can require long distance movements, since spawning habitat and feeding habitats of adults and juveniles may differ (Schlosser, 1991). Although many mussel–host fishes are sedentary, some host fish do migrate long distances. For example, channel catfish (*Ictalurus punctatus*) in the Wisconsin River occupy small home ranges in summer, but migrate downstream into the Mississippi River in fall, and back up the Wisconsin River in spring to spawn at the same summer home sites (Pellett et al., 1998). Gar and freshwater drum also typically swim over long distances (Minns, 1995; Snedden et al., 1999; Albanese et al., 2009).

Long distance movements would have been missed by the spatial and temporal extent of our study, which was restricted to 100-m reaches. Marked fish could have moved out of the study reaches before recapture in subsequent weeks, imposing a bias toward the recapture of stationary individuals. In addition, fish that did not move during our summer study period could have moved during other times of year. Because of logistical constraints, most studies of fish movement have had limited spatial extents. Studies conducted at larger spatial scales have found that fishes such as salmonids can move substantial distances, and that such movement can be common and important

(Gowan et al., 1994; Gowan & Fausch, 1996). Recently, researchers have found that many fish populations are heterogeneous and composed of stationary and mobile components, with the stationary component comprising the largest proportion of the population. For example, Rodriguez (2002) found a median displacement distance of <100 m for twenty-four populations that was typically <50 m, and the proportion of mobile individuals was low in most populations (median 19%). Displacement of mobile individuals was hundreds of meters (median 328.5 m) and eighteen times higher than that of stationary individuals (median 17.9 m). Similarly, Radinger & Wolter (2014) found fish to be partially constrained to a core range in the immediate environment, but also to be straying to distant locations to explore new habitats. Their comprehensive meta-analysis using 160 empirical data sets from 71 studies covering 62 stream fishes found a median movement distance of the mobile component of 361.7 m, whereas that of the stationary component was 36.4 m, with a median share of 66.6% (Radinger & Wolter, 2014). Our study likely represents an accurate measure of common, stationary individuals, but might underestimate movement of rarer individuals that move over long distances, since recording such movements was beyond the scale of our study.

The small proportion of fish hosts that move long distances should be of great importance for mussel dispersal (Horký et al., 2014). Mussel beds represent local subpopulations that are linked into a larger metapopulation through infrequent dispersal (Vaughn, 1993; Newton et al., 2008; Vaughn, 2012). Mussels are long lived (15–40 years on average, but up to 200 years) (Strayer, 2008; Haag & Rypel, 2011; Haag, 2012). The genetic similarity of subpopulations may be the result of spatially limited, but temporally prolonged dispersal of relatively few individuals over long time periods (Nagel, 2000; Elderkin et al., 2007). Dispersal and gene flow among mussel populations is a function of fish movement, which in turn determines mussel distribution (Lee et al., 1998; Vaughn & Taylor, 2000; Zanatta & Murphy, 2006; Vaughn, 2012). For example, mussels that have darters as their hosts frequently form genetically isolated subpopulations (Berg et al., 2007), while those with mobile hosts tend to form more homogenous populations (Berg et al., 1998). Although our findings indicate limited mussel dispersal via fish movement in the Little River, the subpopulations have

been shown to be genetically connected (Reagan, 2008). Cureton & Vaughn (unpublished data) found that genetic connectivity between subpopulations of the threeridge mussel (*Amblema plicata*) in the Kiamichi River is maintained by the movement of ~3.5 propagules per generation. Genetic connectivity of mussel populations likely depends on many factors such as mussel habitat suitability and spatial configuration and host fish identity, abundance, and behavior (Roe et al., 2001; Kelly & Rhymer, 2005; Berg et al., 2007; Newton et al., 2008).

Their relative immobility, long lifespan, and specific reproductive characteristics make freshwater mussels particularly vulnerable to disturbance such as habitat fragmentation (Strayer, 2008). Southeastern Oklahoma experienced severe drought conditions in the summer of 2011, which was reflected by low discharge and a continuing reduction of water depths in the Little River (Atkinson et al., 2014). We found that the mean number of fish captured decreased with decreasing discharge over our study period. When discharge increased at the end of the study because of a rain event, our capture rate increased. Low water levels can force host fish to seek refugia in deep pools (Sedell et al., 1990; Schlosser, 1991; Schaefer et al., 2003), which is likely what occurred in our study. The chances for glochidia attachment and survival of juveniles are greatly reduced in deep pools (Neves & Widlak, 1987). Droughts in this region are predicted to become more frequent and severe with climate change (Seager & Vecchi, 2010), all while the human population grows and uses more water (Sabo et al., 2010). This will likely continue to negatively impact both mussels and their host fishes.

In summary, we found that fishes that are hosts to mussels in the Little River moved little during the summer. When they did move, fish moved more upstream than downstream, allowing mussels to compensate for downstream displacement. Changes in flow conditions in the context of global climate change and water diversion for human use will likely continue to negatively affect mussels and their hosts, including mussel dispersal potential and metapopulation structure. Future studies will need to further investigate the complex interactions between mussels and fish, including the co-evolution of the life histories of these two animal groups and effects on mussel dispersal, spatial distribution patterns, and the genetic connectivity of mussel metapopulations in rivers.

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