Movement patterns and dispersal potential of Pecos bluntnose shiner (Notropis simus pecosensis) revealed using otolith microchemistry


Abstract: Natal origin and dispersal potential of the federally threatened Pecos bluntnose shiner (Notropis simus pecosensis) were successfully characterized using otolith microchemistry and swimming performance trials. Strontium isotope ratios (87Sr:86Sr) of otoliths within the resident plains killifish (Fundulus zebrinus) were successfully used as a surrogate for strontium isotope ratios in water and revealed three isotopically distinct reaches throughout 297 km of the Pecos River, New Mexico, USA. Two different life history movement patterns were revealed in Pecos bluntnose shiner. Eggs and fry were either retained in upper river reaches or passively dispersed downriver followed by upriver movement during the first year of life, with some fish achieving a minimum movement of 56 km. Swimming ability of Pecos bluntnose shiner confirmed upper critical swimming speeds (U_{crit}) as high as 43.8 cm·s$^{-1}$ and 20.6 body lengths·s$^{-1}$ in 30 days posthatch fish. Strong swimming ability early in life supports our observations of upriver movement using otolith microchemistry and confirms movement patterns that were previously unknown for the species. Understanding patterns of dispersal of this and other small-bodied fishes using otolith microchemistry may help redirect conservation and management efforts for Great Plains fishes.

Résumé : L’origine natale et le potentiel de dispersion du méné (Notropis simus pecosensis), une espèce menacée au niveau fédéral, ont été caractérisés avec succès par la microchimie des otolithes et des essais de performance natatoire. Les rapports d’isotopes de strontium (87Sr:86Sr) des otolithes chez le fondule résident (Fundulus zebrinus) ont été utilisés comme substituts des rapports d’isotopes de strontium dans l’eau et ont révélé trois tronçons distincts sur le plan isotopique le long de 297 km de la rivière Pecos (Nouveau-Mexique, États-Unis). Deux motifs distincts de déplacements associés au cycle biologique ont été découverts chez méné. Les œufs et les alevins étaient soit retenus dans des tronçons supérieurs de la rivière ou dispersés passivement vers l’aval pour ensuite se déplacer vers l’amont durant la première année de vie, le déplacement minimum de certains poissons atteignant 56 km. La capacité natatoire de méné a confirmé des vitesses de nage critiques supérieures (U_{crit}) pouvant atteindre 43,8 cm·s$^{-1}$ et 20,6 longueurs du corps·s$^{-1}$ 30 jours après l’éclosion des poissons. Une bonne capacité natatoire tôt durant la vie appuie nos observations de déplacements vers l’amont obtenues de la microchimie des otolithes et confirme des motifs de déplacement jusqu’ici inconnus pour cette espèce. La compréhension des motifs de dispersion de cette espèce et d’autres poissons à petit corps à l’aide de la microchimie des otolithes pourrait aider à réorienter les efforts de conservation et de gestion des poissons des grandes plaines de l’Ouest. [Traduit par la Rédaction]

Introduction

Rivers throughout the southwestern Great Plains have experienced dramatic changes in flow regimes over the last 100 years. These changes are the result of damming; channelization; water diversion; groundwater pumping for municipal, industrial, and agricultural uses; and frequent and persistent droughts (Dodds et al. 2004; Hoagstrom et al. 2008b; Durham and Wilde 2009). The results of flow intermittency and decreased habitat complexity have negatively affected pelagic broadcast spawning fishes (Bestgen et al. 1989; Durham and Wilde 2009; Hoagstrom et al. 2011). For these fishes, spawning occurs throughout the summer and is cued to not only high-flow events (synchrony), but across a range of flow conditions. This spreads reproduction throughout a season, resulting in multiple opportunities (asynchrony) as a hedging strategy to increase chances of young surviving to recruitment (Durham and Wilde 2005; Durham and Wilde 2008).

Broadcast spawning fishes utilize a reproductive strategy in which the female releases ova into the water column whereupon the male(s) fertilize them. The eggs are nonadhesive and semi-buoyant, and as long as water velocity is sufficient, the propagules will remain suspended within the water column and drift downriver while development occurs (Platania and Altenbach 1998; Cowley et al. 2009). Retention of eggs and fry in slack-water nursery habitat reduces the chances of continued downriver displacement and may be key to successful recruitment into the population (Dudley and Platania 2007; Hoagstrom and Turner 2015). In contrast, eggs and fry are at risk if swept into unfavorable habitat such as irrigation canals or into large impoundments where they would perish (Dudley and Platania 2007). Thus, understanding life history movement patterns of broadcast spawning fishes in response to both natural and anthropogenic factors may assist in management and recovery efforts for these fishes.


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In the Pecos River, New Mexico, channel scouring and altered flow regimes from water diversions, channelization, and large impoundments threaten a guild of broadcast spawning fishes that include native speckled chub (Macrhybopsis aestivalis), Rio Grande shiner (Notropis jemezus), and Pecos bluntnose shiner (Notropis simus pecosensis; Platania and Altenbach 1998; Dudley and Platania 2007; Hoagstrom et al. 2011). Of conservation interest is the federally threatened Pecos bluntnose shiner. Once found throughout 631 km of the Pecos River, the fish is now restricted to only 330 km (Platania 1995; Hoagstrom 2003a; Hoagstrom et al. 2008a). The species was state-listed by New Mexico as endangered in 1975 (NMDFG 2012) and federally listed as threatened in 1987 (USFWS 1987), with a lifespan of 2 to 3 years in the wild (Hatch et al. 1985; Bestgen and Platania 1990; Hoagstrom et al. 2008b). From May through the end of September, spawning was historically cued by high-flow events from snowmelt runoff and summer monsoon rains that increased flow from a few hours to a few days. Spawning cues currently include summer precipitation, large volume of long duration water release from a large impoundment (Sumner Dam), and flooding from nonregulated tributary inputs (Hatch et al. 1985; Hoagstrom et al. 2008b).

Persistence of Pecos bluntnose shiner is dependent upon the dispersal and hatch of eggs and whether larvae find refuge in nursery habitat. Without an understanding of dispersal patterns or movement related to reproduction and eventual recruitment of this fish, biologists can only presume environmental variables that limit successful reproduction and recruitment. Unfortunately, little is known of passive dispersal of egg and larvae as well as movement patterns of this species (Platania and Altenbach 1998; Hoagstrom et al. 2008a, 2008b). Movement of juvenile and adult Pecos bluntnose shiner have not been studied in depth; however, some notable size reduction downriver has been documented (Hoagstrom et al. 2008b). The absence of adult Pecos bluntnose shiner in the southern-most occupied portion of the river above Brantley Reservoir suggests that fish in this lower area are either not recruiting into the population or are not surviving to maturity (Hoagstrom et al. 2008b). In addition, source areas where propagules deposit and larvae develop to eventually recruit into the core population are unknown (Platania and Altenbach 1998; Hoagstrom et al. 2008a). Ultimately, recruitment of Pecos bluntnose shiner is dependent upon where eggs disperse and hatch and if larvae find refuge. If the source of recruitment comes from downriver, those individuals likely must swim upriver to successfully reproduce or their eggs potentially disperse further downriver into Brantley Reservoir (Platania and Altenbach 1998; Dudley and Platania 2007). The success of this fish is further complicated by the timing and magnitude of water release from Sumner Dam to reduce evaporative loss between reservoirs and efficient water delivery for agricultural use. Without knowing dispersal patterns or movement related to reproduction of the species, managers could only presume environmental variables that affect successful reproduction and recruitment.

Future management efforts targeted at improving and facilitating life history movement patterns of Pecos bluntnose shiner may aid in its recovery. However, little is known about movement patterns and dispersal potential of this species after larval development. The objectives of this research were to (i) assess the direction and extent of potential dispersal of Pecos bluntnose shiner by reconstructing natal origin using otolith microchemistry of strontium isotopes ($^{87}$Sr/$^{86}$Sr) from hatch until time of capture and (ii) perform controlled swimming performance trials to better understand age-related dispersal potential in this species. Understanding life history movement patterns in Great Plains fishes is an essential step in developing conservation strategies and guiding informed management actions to ensure persistence of this unique guild of broadcast spawning fishes.

Materials and methods

Study area

Currently, the Pecos bluntnose shiner is restricted to the Pecos River main stem from Sumner Dam to Brantley Reservoir, a distance of 330 km within three distinct areas (Tailwater, Rangelands, and Farmlands; Fig. 1; Hoagstrom 2003a, 2003b). The Tailwater area is the most northern portion of the river between Sumner Dam and the confluence of the Pecos River at Taiban Creek and extends 33 km (Fig. 1). Release of sediment-free water from Sumner Dam leads to channel scour creating unsuitable habitat where the species has not been collected since 1999 (Hoagstrom 2003a; Hoagstrom et al. 2008b; Davenport 2010). The middle section (Rangelands) is characterized as having the most suitable fish habitat of shifting sand-bed and a braided river channel extending from Taiban Creek to the Rio Hondo confluence for a total of 155 km (Fig. 1). Adult size classes of Pecos bluntnose shiner have been routinely documented within this area of the river (Hoagstrom 2003a, 2003b). The southernmost section (Farmlands) extends from the Rio Hondo confluence to Brantley Reservoir for a total of 142 km (Fig. 1) and is characterized as a deeply incised narrow channel with a compacted river bed, modified for more effective water delivery (Tashjian 1993). Salinity is elevated in this lower area owing to the cumulative effects of diminished stream flow, increased evapotranspiration, saline irrigation return flows, and brine aquifer intrusion (Hoagstrom et al. 2008a; Hoagstrom 2009).

Adult Pecos bluntnose shiner are generally absent from this most southern area (Hoagstrom et al. 2008b).

Bedrock and Pecos River water chemistry

A geologic map of the study area revealed unique differences in bedrock formation throughout the Pecos River drainage (NMBGR 2003). The dominant bedrock throughout the northern section of the river is reflected by the Guadalupian Formation from the Permian period (270–260 million years ago). In contrast, the dominant bedrock throughout lower reaches of the river is reflected by Piedmont alluvial slopes from the Holocene to early Permian period (270–260 million years ago). These formations consist of carbonate (limestone and dolomite) and evaporite (gypsum and halite). Thus, older bedrock in the northern portion of the river is reflected by higher $^{87}$Sr/$^{86}$Sr values, while younger bedrock in the southern portion of the river is reflected by lower $^{87}$Sr/$^{86}$Sr values (Barnett-Johnson et al. 2008; Hegg et al. 2013).

A total of four water samples were collected 23–25 April 2012 during base flows as an initial assessment of $^{87}$Sr/$^{86}$Sr values. The four sample locations were predecisional in an attempt to locate differences in $^{87}$Sr/$^{86}$Sr reflecting dominant bedrock. Thus, two water samples were collected from the most northern sampling sites within the Rangelands area at Willow and Highway 70, and two water samples were collected in the most southern sampling sites within the Farmlands area at Dexter and Highway 82 (Fig. 1). The water samples were analyzed using inductively coupled plasma mass spectrometry (ICPMS) at the University of California-Davis Interdisciplinary Center for Plasma Mass Spectrometry.

Fish collection and otolith preparation

The plains killifish (Fundulus zebroides) is present throughout the home range of the Pecos bluntnose shiner and rarely exhibits large-scale patterns of movement (Minkelley and Klaassen 1969). We chose to use otolith $^{87}$Sr/$^{86}$Sr values from the plains killifish as our reference (or surrogate) for $^{87}$Sr/$^{86}$Sr in water as a more cost-efficient alternative to characterize $^{87}$Sr/$^{86}$Sr values throughout...
the range of the Pecos bluntnose shiner. As a resident, the plains killifish would presumably capture ambient water chemistry at a particular location (from time of hatch to time of capture). Thus, a range of sizes of plains killifish (n = 97, range 19.4–55.4 mm standard length, SL) were collected 7–9 November 2012 using a 3.0 m × 1.2 m seine with 3.2 mm mesh. From north to south, the sample collection sites were Willow, 6 Mile Draw, Crockett Draw, Bosque, Gasline, Highway 70, Dexter, Lake Arthur Falls, and Highway 82 (Fig. 1).

Pecos bluntnose shiner were sampled on the same sample dates and within the same sample sites as the plains killifish. A range of sizes of Pecos bluntnose shiner (n = 119, range 29.7–60.1 mm SL) were also collected. From north to south, the collection sites were Willow, 6 Mile Draw, Crockett Draw, Bosque, Gasline, Highway 70, and Dexter (Fig. 1). Pecos bluntnose shiner were absent from sample collections at Lake Arthur Falls and Highway 82 (Fig. 1). Fish were collected just before the onset of winter to ensure sufficient growth of young-of-year fish for capture in seines and to detect movement using otoliths. Captured fish were euthanized, placed on dry ice, and transported to the laboratory. Sagittal otoliths were removed, placed into 1.5 mL vials with ultrapure (milli-Q) water, and cleaned using an ultrasonic, ultrapure water bath for 5 min to remove organic tissue. Otoliths were then rinsed again with ultrapure water, placed in new 1.5 mL vials, and al-
lowed to dry under a class 100 laminar-flow hood. After 48 h dry time, otoliths were mounted sulcus side up, affixed to a microscope slide with Crystalbond (Crystalbond 509, Ted Pella Inc., Redding, California), and sanded using a MTI Corporation UNIPOL 1210 grinding–polishing machine (1200 grit sand paper wetted with ultrapure water) to reveal the core to the edge (Thorrold et al. 1998; Hobbs et al. 2010).

Laser ablation multicollector inductively coupled mass spectrometer (LA-ICPMS) was used to assess $^{87}\text{Sr}/^{86}\text{Sr}$ in otoliths. Analysis was conducted at the University of California-Davis Interdisciplinary Center for Plasma Mass Spectrometry using a New Wave Research UP213 laser ablation system coupled with a Nu Plasma HR (Nu322) multiple-collection, high-resolution, double-focusing plasma mass spectrometer system. Line scans across the face of the otolith from the core to the edge generated $^{87}\text{Sr}/^{86}\text{Sr}$ profiles throughout the fish’s life. A scanning speed of 10 $\mu$m·s$^{-1}$, beam width of 40 $\mu$m, laser pulse frequency of 10 Hz, and 65% laser power were used. Values for $^{87}\text{Sr}/^{86}\text{Sr}$ were normalized in relation to $^{87}\text{Sr}/^{88}\text{Sr}$ (0.1135) to correct for instrumental mass fractionation. Instrumental accuracy was ensured using a modern marine coral (an in-house calcium carbonate standard).

Aging

After isotopic analysis, otoliths were photographed using a Leica DME microscope with Leica ICC50 Camera Module and Leica Live Image Building Software (LAS Software Version 4.4.0, Heerbrugg, Switzerland) to generate whole otolith photographs. Data from the isotopic analysis were overlaid following the ablation path for each otolith, and the ages at which isotopic shifts occurred were then recorded for each fish. Otolith photographs were viewed by two independent analysts, and assigned ages were compared (Miller and Storck 1984). Briefly stated, where age discrepancy occurred at greater than 10%, a third analysis was performed and ages were accepted if the third age analysis fell within 10% of the first two aging attempts. If consensus could not be reached, age for that fish was excluded. Of the total Pecos bluntnose shiner collected ($n = 119$), five fish could not be aged and were excluded from the age classification.

Age at movement

For each Pecos bluntnose shiner, the age at which an isotopic shift occurred from laser ablation analysis was identified from digital images using ImageJ software (version 1.48i, National Institute of Health). Distance ($\mu$m) was calibrated using known length laser ablation line recorded during $^{87}\text{Sr}/^{86}\text{Sr}$ analysis. Fish growth varies between the warmer summer months (majority of growth occurring during this season) and cooler autumn–winter (growth is slow). Daily rings were easily counted the first year of life. Thus, age at which fish moved was binned into groups, with 0+early representing within 30 days posthatch, 0+mid representing 30–60 days posthatch, 0+late representing from 60 days posthatch to pre-annulus formation, 0+winter representing within the first annulus (winter), 1+early representing early growth after winter (second growing season), 1+mid representing midsummer growth (second growing season), and 1+late representing late summer–fall growth (second growing season).

Swimming performance

Captive propagated Pecos bluntnose shiner were tested at 30 days ($n = 30$, mean 20.63 mm total length, TL), 60 days ($n = 30$, mean 33.93 mm TL), 90 days ($n = 15$, mean 46.33 mm TL) posthatch and wild-caught adults ($n = 30$, 69.13 mm TL) from the Pecos River using a swim tunnel (Loligo Systems, Denmark). Fish younger than 30 days posthatch could not be tested with the stamina tunnel (several 30-day fish escaped from the stamina tunnel resulting in test termination and were not included in calculations). Water quality was monitored and maintained such that it did not influence swimming performance among age classes. Fish were acclimated at 1.0 cm·s$^{-1}$ flow 1 week prior to the swimming trials. On test day, individual fish were placed in the stamina tunnel and allowed to acclimate for 1 h at 5.0 cm·s$^{-1}$. Flow was increased by 10.0 cm·s$^{-1}$ increments at 5 min intervals until the fish fatigued and became pinned against the back screen for more than 5 s (conclusion of the test). At the termination of each test, fish were measured for total and standard lengths (mm) and placed into a recovery tank. Critical swimming speed ($U_{crit}$) was calculated using the equation from Beamish (1978):

$$U_{crit} = U_{i} + [(1 - t_{i}/t_{f})] \times U_{n}$$

and body lengths per second

$$B_{L} = U_{crit} \cdot TL$$

where $U_{i} =$ the full interval swam at the highest velocity (cm·s$^{-1}$), $U_{n} =$ the velocity increment (cm·s$^{-1}$), $t_{i} =$ time (s) fish swam in the final increment until becoming pinned, $t_{f} =$ duration of each increment, and TL = total length of individual fish.

Data analysis

For both species, a ten-point moving average was used to smooth the $^{87}\text{Sr}/^{86}\text{Sr}$ values for visual inspection. The fish was deemed a resident if no isotopic shifts were evident through visual inspection of the full data profiles matching one location throughout the fish’s life and by comparing means between halves of the line scans for each fish via t tests (JMP, version 10, SAS Institute Inc.). When $^{87}\text{Sr}/^{86}\text{Sr}$ values revealed an isotopic shift (i.e., clear breakpoint in the data indicating different reaches), then it was presumed the fish moved between areas of unique $^{87}\text{Sr}/^{86}\text{Sr}$ chemistry. For example, an upriver movement was identified if isotopic values near the otolith core were classified to downriver reaches and isotopic values near the otolith edge were classified to upriver reaches, or vice versa. When an isotopic shift was evident, isotopic values representing each location were partitioned separately because fish were presumed to have spent time within an isotopically distinct reach. We verified breakpoints in the $^{87}\text{Sr}/^{86}\text{Sr}$ values for each fish using a Student’s t test to determine if pre- and postbreakpoints were significantly different. For fish exhibiting two or more breakpoints, we used an analysis of variance (ANOVA) to test for significant differences and Tukey’s post hoc to determine where differences occurred (JMP, version 10, SAS Institute Inc.).

Discriminant function analysis was conducted to determine whether $^{87}\text{Sr}/^{86}\text{Sr}$ values could be used to correctly classify individual fish to the river reach of their capture location (PROC DISCRIM, version 9.3, SAS Institute Inc.). First, $^{87}\text{Sr}/^{86}\text{Sr}$ data from plains killifish were used as a training data set to classify all fish into one of three isotopically distinct reaches of the River. The jackknife resampling procedure was used for plains killifish data in a cross-validation technique (one observation is left out) to assess model validity by comparing the predicted with known capture location. Second, we classified otolith microchemistry edge readings of Pecos bluntnose shiner to capture locations, which we compared with known capture locations to assess classification success. Third, we classified core and middle $^{87}\text{Sr}/^{86}\text{Sr}$ values to the three isotopically distinct areas to determine movement patterns for each Pecos bluntnose shiner. In all cases, we used a probability of 0.5 as the cutoff for classification of location. Unequal within-group covariance was used owing to failure of the test for equal within-group covariance ($\chi^{2} = 10.14$, $p = 0.006$).
Fig. 2. Plains killifish (diamonds) were used as a surrogate for identification of shifts in $^{87}$Sr:$^{86}$Sr values from the northern to the southern end of our study area in the Pecos River. Otolith $^{87}$Sr:$^{86}$Sr values from plains killifish revealed a distinct shift at Highway 70. The intermediate and more variable $^{87}$Sr:$^{86}$Sr values observed at Highway 70 indicate a shift in water microchemistry as the bedrock geology changes near this site. Bars represent mean (±2 standard errors) of $^{87}$Sr:$^{86}$Sr otolith values, and mean $^{87}$Sr:$^{86}$Sr values for plains killifish from upriver and downriver sites is depicted by the two dashed lines. Circles represent $^{87}$Sr:$^{86}$Sr values of four water samples collected at Willow (0.7083), Highway 70 (0.7082), Dexter (0.7078), and Highway 82 (0.7078).

Results

Water chemistry and otolith microchemistry of plains killifish

Noteworthy differences in $^{87}$Sr:$^{86}$Sr values were observed among the four water samples throughout the upper Rangelands and lower Farmlands area of the Pecos River. Three distinct $^{87}$Sr:$^{86}$Sr values were described supporting differences in geologic rock types. Values for $^{87}$Sr:$^{86}$Sr in water varied from 0.7082 to 0.7083 in the upper Rangelands area (Willow and Highway 70, respectively) and 0.7078 (n = 2) in the lower Farmlands area (Dexter and Highway 82; Fig. 2). These four water samples represented only a snapshot for each location, but were deemed sufficiently different to determine that a movement study for Plains bluntnose shiner was warranted.

Similar to water samples, values for $^{87}$Sr:$^{86}$Sr in otoliths of plains killifish were reflective of an upper reach (Willow, 6 Mile Draw, Crockett Draw, Bosque Draw, Gasline), middle reach (Highway 70), and a lower reach (Dexter, Highway 82) (Fig. 2). In addition, no seasonal shifts in isotopic values of the Pecos River were detected as indicated by the stability of laser ablation path $^{87}$Sr:$^{86}$Sr values from the primordia to the edge of each plains killifish otolith. Of plains killifish captured above Highway 70 (hereinafter referred to as the upper reach), 91% (50/55) were classified correctly as originating in that reach, 56% (5/9) were classified correctly to Highway 70, reflecting a transition or mixing zone, and all 33 (100%) plains killifish captured below Highway 70 (hereinafter referred to as the lower reach) were classified correctly. Thus, the plains killifish was deemed a suitable surrogate for characterizing Pecos River water $^{87}$Sr:$^{86}$Sr throughout the study area both spatially (all sites where fish were captured) and temporally (throughout the lives of the fish). As such, additional water samples were not collected to ensure correct classification because of cost considerations and because plains killifish otolith isotope values from the primordia to the edge closely reflected water samples collected throughout the three distinct isotopic reaches.

Evaluation of Pecos bluntnose shiner classifications

Discriminant function analysis of otolith $^{87}$Sr:$^{86}$Sr edge values indicated that 74% (75/101) of the Pecos bluntnose shiner were correctly assigned to the upper reach. Twenty-six percent (26/101) of fish were misclassified as captured at Highway 70. Seventy-five percent (3/4) of Pecos bluntnose shiner from the lower reach were correctly assigned to the lower reach, while one was misclassified to Highway 70. Only 36% (5/14) of the fish were correctly assigned to Highway 70. Six fish were misclassified to the upper reach when they should have been classified to Highway 70. Three fish were misclassified to the lower reach when they should have been classified to Highway 70. Classification of fish to Highway 70 had greater inherent error as a transition zone of isotopic values because of the shift in bedrock above and below the area.

Reconstructing natal origin and movement of Pecos bluntnose shiner

Otolith primordia or early life $^{87}$Sr:$^{86}$Sr values revealed natal origins for the majority (82%, 83/101) of Pecos bluntnose shiner began in the middle and lower reaches (Table 1). Prior to capture at the upper-most site (Willow) in the upper reach, 22% (7/32) of Pecos bluntnose shiner began early life in the upper reach, 25% (8/32) of these fish began early life in the middle reach, while 53% (17/32) began early life in the lower reach. Thus, 82% of Pecos bluntnose shiner hatched at, or below, Highway 70, while 18% hatched in the upper reach and remained in the upper reach until capture at Willow. Fish captured at Gasline, Highway 70, and Dexter sites contained no primordia with $^{87}$Sr:$^{86}$Sr values representative of natal origins within the upper reach, indicating these fish hatched at, or below, Highway 70 (Table 1).

$^{87}$Sr:$^{86}$Sr values revealed fewer fish were residents throughout their lives within the upper reach. After reconstructing movement patterns using otolith $^{87}$Sr:$^{86}$Sr values, the majority of Pecos bluntnose shiner captured at sites within the upper reach had moved to the upper reach from either Highway 70 or from the

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lower reach. Of the total fish captured within the upper reach, 18% (18/101) were life-long residents within the upper reach (Table 2). In contrast, 82% (83/101) of the total fish captured within the upper reach had moved to this reach from either Highway 70 or from the lower reach. $^{87}$Sr:$^{86}$Sr values also revealed large dispersal distances of Pecos bluntnose shiner. For example, the minimum distance was 56 km from Highway 70 for movement of nonresident fish captured at the Willow site (Table 2).

**Table 2. Resident and upriver movement of Pecos bluntnose shiner before capture within the upriver reach (above Highway 70).**

<table>
<thead>
<tr>
<th>Capture site</th>
<th>Residents within upper reach</th>
<th>Movement upriver from Highway 70 or lower reach</th>
<th>Distance moved upriver from Highway 70 (river kilometres)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Willow</td>
<td>22% (7/32)</td>
<td>78% (25/32)</td>
<td>56</td>
</tr>
<tr>
<td>6 Mile</td>
<td>16% (3/19)</td>
<td>84% (16/19)</td>
<td>45</td>
</tr>
<tr>
<td>Crockett</td>
<td>13% (3/23)</td>
<td>87% (20/23)</td>
<td>37</td>
</tr>
<tr>
<td>Bosque</td>
<td>22% (5/23)</td>
<td>78% (18/23)</td>
<td>27</td>
</tr>
<tr>
<td>Gasoline</td>
<td>0% (0/4)</td>
<td>100% (4/4)</td>
<td>11</td>
</tr>
<tr>
<td>Willow</td>
<td>18% (18/101)</td>
<td>82% (83/101)</td>
<td>—</td>
</tr>
</tbody>
</table>

**Discussion**

Isotopic chemistry of the Pecos River across all sampling locations was successfully characterized both spatially and temporally using $^{87}$Sr:$^{86}$Sr values from otoliths of the less mobile plains killifish. Strontium values in otoliths of plains killifish revealed these fish remained within isotopically unique river reaches and that there were no detectable seasonal shifts within the study area. Isotopically unique reaches encompassed larger areas than movements made by resident plains killifish, thus allowing the use of $^{87}$Sr:$^{86}$Sr in plains killifish otolith as a suitable surrogate for $^{87}$Sr:$^{86}$Sr in water. Resident fishes have utility in assessing movements of mobile fishes using $^{87}$Sr:$^{86}$Sr values in otoliths especially if variability of $^{87}$Sr:$^{86}$Sr values through time can be accounted for (Gillanders 2002). Thus, the mixing zone at Highway 70 represented the confluence of two distinctive bedrock geologies, and while this area of transition resulted in less certainty for classifying movement, the use of a resident fish improved classification of movement.

Pecos bluntnose shiner exhibited two patterns of movement that may explain recruitment into the population. The first more common pattern was passive dispersal of propagules downstream below Highway 70, followed by movement upriver prior to their first winter (82% of fish captured above Highway 70). The second less common pattern was passive dispersal with retention of propagules in the upriver reach where residents remained at or above Highway 70 throughout their lives (18% of the fish captured at or above Highway 70). Cowley et al. (2009) suggested that bidirectional dispersal (downriver displacement and upriver movement) was important in the life history of a similar Great Plains river fish (Rio Grande silvery minnow, Hybognathus amarus). The combined return of young-of-year from downriver and retention as residents suggests that the current success of the population relies on eventually securing a large portion of the population through egg retention in the upriver reach. Downriver displacement of propagules is advantageous in fishes of Great Plains rivers with variable flow regimes and long unobstructed stretches. Movement performed better at higher flow rates (Table 3). When considering size of fish, higher swimming rate (BL$^{-1}$) was observed in the youngest fish (30 days posthatch) (Table 3). Total distance swam was also calculated during swimming trials, revealing fish at 30 days posthatch swam a distance of 0.55 km in 83 min and adult fish swam a distance of 1.04 km in 96 min. Water quality was within acceptable limits throughout all swimming challenges. Water temperature varied from 19.7 to 20.6 °C, dissolved oxygen varied from 7.32 to 7.83 mg·L$^{-1}$, pH varied from 7.51 to 7.74, and conductivity varied from 2.26 to 2.31 mS·cm$^{-1}$.

### Swimming performance tests of Pecos bluntnose shiner

Swimming performance tests of Pecos bluntnose shiner supported our reconstruction of movement from $^{87}$Sr:$^{86}$Sr values in otoliths. Even at an early age of 30 days posthatch, these fish exhibited a strong swimming capacity. Upper critical swimming speed ($U_{cri}$) increased with total length, indicating that larger fish
upriver for spawning by adult fish ensures adequate distance for egg drift and development downriver (Cross et al. 1985; Durham and Wilde 2008). However, discharge, habitat complexity, and fragmentation ultimately affect egg retention. Using gellan beads as egg surrogates, Dudley and Platania (2007) demonstrated transport distances of propagules from pelagic broadcast spawning fishes might occur three times further during sustained reservoir releases. Additionally, Worthington et al. (2014) demonstrated downstream drift of egg surrogates was driven by increased velocity but that as habitat complexity increased, a larger proportion of eggs were retained. Within the Pecos River, if propagules are not deposited into slack-water nursery habitat, then young fish are eventually at risk of downriver displacement and removal from the population (Brooks et al. 1994; Platania and Altenbach 1998). Hoagstrom et al. (2008a) related high densities of young Pecos bluntnose shiner at the inflow of Brantley Reservoir to a long release of water from Sumner Dam.

Successful fish movement upriver and maintaining position in flow rely on fish size and behavior (Ward et al. 2003) as well as flow velocity and channel morphology (Leavy and Bonner 2009).
Pecos bluntnose shiner prefer shallower depths coupled with relatively swift water velocity typical of wide shifting sand-bed rivers (Hoagstrom et al. 2008a). Hoagstrom et al. (2008b) associated length classes of Pecos bluntnose shiner with water velocity and found a positive relationship between increasing water velocity and fish size. Upper critical swimming speeds ($U_{\text{crit}}$, 43 cm·s$^{-1}$) for Pecos bluntnose shiner as young as 30 days posthatch revealed the upper threshold of aerobic swimming capacity is high for this species at an early age. Caldwell et al. (2010) reported 34.3–44.1 cm·s$^{-1}$ for upper critical swimming speed in Rio Grande silvery minnow at 116 days posthatch. In comparison, Pecos bluntnose shiner exhibited higher swimming capacity ($U_{\text{crit}}$, 52.5 cm·s$^{-1}$) at 90 days posthatch. Bestgen et al. (2010) reported upper critical swimming speeds of 51.5 cm·s$^{-1}$ (53–75 mm TL) for Rio Grande silvery minnow, noting that swimming ability increased with fish size. Although Pecos bluntnose shiner demonstrated strong swimming ability and upriver movement, downriver dispersal of propagules has potentially tripled to distances up to 142 km from predam–prechannelization of the river (Dudley and Platania 2007).

Persistence of Pecos bluntnose shiner relies on a variety of abiotic factors that include timing of pulse flows that cue spawning events, habitat quality, and perennial flow to maintain river connectivity for bidirectional dispersal to complete their life cycle. Using otolith microchemistry, we recorded that movement in the population coincided with years of perennial flow throughout summer and fall (fish hatched 2010 and 2011) before the onset of their first winter. During the study (2011–2012), the Southwest experienced one of the most severe droughts on record (http://www.droughtmonitor.unl.edu/archive.html, accessed 10 November 2012). Our capture and otolith analysis revealed that when river conditions supported fish spawning and movement, the 2008 age class 0+ represented 16%–51% of Pecos bluntnose shiner collected throughout the reaches of the river.

Otolith $^{87}$Sr:$^{86}$Sr values revealed new information on life history movement patterns of a small-bodied but highly mobile fish. As a relatively short-lived species, Pecos bluntnose shiner must move upriver early in life such that when the opportunity to spawn occurs, propagules have sufficient distance to drift while developing. Swimming performance tests confirmed that young Pecos bluntnose shiner were capable of moving upriver prior to their first winter where they gain reproductive advantage of the dispersal distance for propagule development. These movement patterns represent a trade-off between years with stream drying in upper sections and the minimum distance needed for adequate development (i.e., bet-hedging strategy). Habitat restoration in the southern Farmlands area of the Pecos River would likely benefit pelagic spawning fish by returning this area from a highly modified channel to braided, more complex areas with shifting sand-bed. This would increase backwater areas for nursery habitat and thereby increase chances of success for the return of the Pecos bluntnose shiner to the upper reach and completion of its life history.

### Table 3. Mean total length (TL, mm), critical swimming speed ($U_{\text{crit}}$, cm·s$^{-1}$), swimming rate (body lengths (BL)·s$^{-1}$), and mean total distance swam (km) of four age classes of Pecos bluntnose shiner.

<table>
<thead>
<tr>
<th>Age class</th>
<th>TL (mm)</th>
<th>$U_{\text{crit}}$ (cm·s$^{-1}$)</th>
<th>BL·s$^{-1}$</th>
<th>Total distance (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>30-day</td>
<td>21.3 (0.62)</td>
<td>43.8 (4.46)</td>
<td>20.6 (2.02)</td>
<td>0.55 (0.094)</td>
</tr>
<tr>
<td>60-day</td>
<td>33.9 (0.92)</td>
<td>49.2 (1.94)</td>
<td>14.5 (0.52)</td>
<td>0.62 (0.031)</td>
</tr>
<tr>
<td>90-day</td>
<td>46.3 (0.82)</td>
<td>52.5 (2.48)</td>
<td>11.3 (0.62)</td>
<td>0.68 (0.042)</td>
</tr>
<tr>
<td>Adult</td>
<td>69.1 (2.28)</td>
<td>70.3 (3.26)</td>
<td>10.2 (0.54)</td>
<td>1.04 (0.074)</td>
</tr>
</tbody>
</table>

Note: Values in parentheses are two standard errors. Sample size of 30 fish was used for 30-day, 60-day, and adult age classes, while 15 fish were tested for 90-day age class.