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TESTING RESTRICTED MOVEMENT OF PLAINS KILLIFISH (*FUNDULUS ZEBRINUS*)

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ABSTRACT—We tested the restricted movement paradigm (RMP) for heterogeneous movement within populations using plains killifish (*Fundulus zebrinus*) in the Red River on the border of Texas and Oklahoma. During June–August 2020, we marked 564 plains killifish within a 5-km stream segment and recaptured 23 individuals. Recaptured individuals spent on average 17.3 days at large, moved on average 178.2 m/day, and the maximum movement observed was 935 m. Distributions of movement distances and movement rates were leptokurtic, and although distributions were skewed, there was no difference in the number of fish that moved upstream versus downstream. Our results suggest the RMP predicts broad-scale movement patterns of *F. zebrinus*, but fine-scale movements might be larger in magnitude compared with other *Fundulus* spp.

RESUMEN—Examinamos el paradigma de movimiento restringido (en inglés, restricted movement paradigm; RMP) para movimiento heterogéneo dentro de poblaciones utilizando a los Killis de las llanuras (*Fundulus zebrinus*) en el río Rojo en la frontera de Texas y Oklahoma. Durante junio–agosto del 2020, marcamos 564 Killis dentro de un segmento de arroyo de 5 km y recapturamos a 23 individuos. Los individuos recapturados permanecieron en movimiento un promedio de 17.3 días, se desplazaron un promedio de 178.2 m/día, y se observó un desplazamiento máximo de 935 m. La distribución de distancias y tasas de movimiento fueron leptocúrticas, y aunque las distribuciones fueron asimétricas no se encontró diferencia en el número de peces que se desplazaron río arriba versus río abajo. Nuestros resultados sugieren que el RMP predice patrones de desplazamiento a amplia escala de *F. zebrinus*, pero desplazamientos a pequeña escala podrían ser mayores que otras especies de *Fundulus*.

Movement by stream fishes was historically considered restricted (Gerking, 1959) despite early observations that some populations were composed of stationary and mobile components (Funk, 1957). Decades after these initial investigations, Gowan et al. (1994) suggested the “restricted movement paradigm” (RMP) in stream fishes was a paradigm lost, because fish dispersal was generally underestimated during movement studies. However, Rodriguez (2002) later emphasized that the RMP was simply incomplete rather than lost given evidence for heterogeneous populations of stream fishes composed of both stationary and mobile components (Skalski and Gilliam, 2000). The current prevailing interpretation of the RMP is that stream fish populations are composed of stationary and mobile components and that movement magnitudes are predictable based on parameters such as

fish size, caudal fin morphology, stream size, and the amount of time fish have to make movements (Radinger and Wolter, 2014; Wells et al., 2017; Aparicio et al., 2018).

The extent to which stream-fish life histories and spawning modes influence movement has recently received increased attention. For example, the guild of freshwater stream fishes known as pelagic broadcast-spawning (PBS) fishes is hypothesized to make long-range movements to compensate for downstream drift during early life stages (reviewed by Worthington et al., 2018). Chase et al. (2015) studied the movement of one such PBS species, the Pecos bluntnose shiner (*Notropis simus pecosensis*), using otolith microchemistry. A critical assumption in the work by Chase et al. (2015) was that strontium isotope ratios from plains killifish (*Fundulus zebrinus*) could be used to reflect local-scale ratios in water

because of restricted lifetime movements by *F. zebrinus*. Although Minckley and Klaassen (1969) anecdotally suggested closely related *Fundulus kansae* are restricted in their movement, no formal analysis of *F. zebrinus* movement has been conducted to our knowledge. The goal of this study was to quantify dispersal patterns of *F. zebrinus* using mark–recapture to assess the mobility of the species and therefore the validity of its presumed restricted movements.

Our study was conducted on a sixth-order (Strahler, 1957) segment of the mainstem Red River near Vernon, Texas, at the U.S. Highway 283 crossing. The Red River in this region is characterized by a braided, meandering sandy bed and unpredictable, seasonal flow variability. The Red River basin averages 82 cm of precipitation per year with arid summer climates increasing toward its western half (Benke and Cushing, 2005). The land use in this area is dominated by agriculture with up to 90% being used for rangeland and crops (Benke and Cushing, 2005). We focused on a 5-km-long segment of stream that was subdivided into five 1-km-long reaches. These reaches included (1) an upstream search reach, (2) an upstream tagging reach, (3) a middle search reach, (4) a downstream tagging reach, and (5) a downstream search reach (Albanese et al., 2003). The tagging reaches (Reaches 2 and 4) were then further subdivided into five 0.2-km subreaches where individuals could be batch-tagged using visible implant elastomer.

We assessed movement of *F. zebrinus* during three tagging and immediate recapture events (16–19 June, 4–6 July, and 21–23 July 2020) plus a final long-distance recapture event (11–12 August 2020). We collected specimens for tagging using three passes of a 9.1×1.8 -m shallow-bag seine with 6.4-mm mesh in each 0.2-km subreach of the two tagging reaches. In the middle of each subreach, we placed a perforated tub in the river with a sandbag weight to hold collected specimens from that subreach until tagging. We monitored short-term mortality by holding fish for ≥ 1 h and noted that mortality occurred in only two individuals, meaning that our tagging did not affect local density. Tagging consisted of injecting visible implant elastomer into the muscles of the fish just under the skin using a 0.3-mL syringe with a 29-gauge, 12-mm-long needle. The visible implant elastomer was injected as the needle was withdrawn, leaving a 2–3-mm streak in the muscle (Olsen and Vllestad, 2001). This tagging procedure lasted < 10 s/tag and preliminary tagging showed low mortality; thus, we did not anesthetize any fish. We measured each tagged fish for total length (in millimeters; Musselman et al., 2017) before placing it in an aerated recovery tub. We recorded global positioning system (GPS) coordinates at each of the 10 subreach release locations. We used a combination of distinct marking colors (purple, white, brown) and fish body locations (five on either side of the body) so that each event and subreach could be identified.

The first three tagging and recapturing events were conducted over the course of 3 days. On the first day we tagged individuals in one of the two tagging reaches, on the second day we tagged individuals in the second tagging reach, and on the third day we searched the entire 5-km segment from upstream to downstream. We alternated which tagging reach was visited first among each of the events. Our final recapture-only event was conducted over a 2-day period and included two extra kilometers upstream and downstream of the focal segment for a total of 9 km. On recapture days, we used a single-pass approach to search the entire segment and recorded GPS coordinates, length, and tag color and body location for each recaptured *F. zebrinus*. We estimated movement distances by calculating the Euclidean distance (meters) along the stream thalweg between mark and recapture GPS points using a geographic information system.

We analyzed *F. zebrinus* movement using multiple analyses. First, we tested for leptokurtosis of pooled (i.e., across all events) movement data and pooled movement rate (i.e., distance/time at large) using Anscombe-Glynn's test implemented with the R function 'anscombe.test' (Anscombe and Glynn, 1983). Second, we tested for upstream or downstream bias in movement rate using a Mann-Whitney *U* test implemented with the 'wilcox.test' function in Program R (Bauer, 1972) and skewness using D'Agostino's test implemented with the 'agostino.test' function in R (D'Agostino, 1970). Third, we tested for relationships between fish size (total length [TL] in millimeters) and either distance moved (meters) or movement rate (meters/day) using linear regression. All of these analyses are commonly used to assess fish movement in streams (Skalski and Gilliam, 2000; Petty and Grossman, 2004; Hudy and Shiflet, 2009; Wells et al., 2017). Finally, we tested whether *F. zebrinus* movements were consistent with the RMP using the R package 'fishmove' (Radinger and Wolter, 2014). The first step in this analysis was to calculate expected movement parameters using the function 'fishmove,' which uses four predictor variables to estimate the distance moved by the stationary component, the distance moved by the mobile component, and the share of the stationary component within the double-normal distribution described by Radinger and Wolter (2014). These distances are estimated using fish TL, stream order (Strahler, 1957), caudal fin aspect ratio (Pauly, 1989), and time at large since tagging (days). We developed estimates for expected movement distances and rates using the mean length of recaptured *F. zebrinus* (53.6 mm TL), stream order = 6, the median caudal fin aspect ratio (1.74) from scientific photographs of *F. zebrinus* by Thomas et al. (2007; ratio = 1.49) and Uland Thomas (<https://gallery.nanfa.org/v/members/Uland/Family+Fundulidae>; ratio = 2.019), and either the average days between tagging and recapture (17 days) for the movement distance analysis or a single day (1 day)

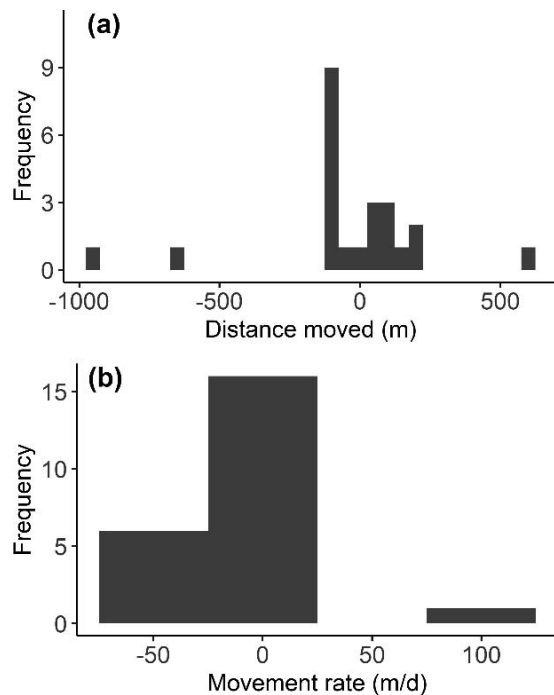


FIG. 1—Frequency distributions of (a) net distance moved and (b) movement rate for 23 *Fundulus zebrinus* recaptured in the mainstem Red River, on the border of Texas and Oklahoma, during June–August 2020. Both distributions are based on 50-m bins.

for the movement rate analysis. The ‘fishmove’ function provides an estimate and 95% confidence intervals, so we compared these expected movement estimates with observed movement parameters derived using the function ‘fishmove.estimate.’ This function fits a double-normal distribution to a vector of field data, and we used either the absolute distance moved or movement rate for each of the recaptured individuals.

We tagged 564 age-0 to age-2 (Ruppel and Bonner, 2020) *F. zebrinus* (length range = 28–70 mm TL) and recaptured 23 (40–70 mm TL). Recaptured individuals spent on average 17.3 days at large and moved on average 178.2 m/day. The Anscombe-Glynn test for kurtosis showed significant leptokurtosis for both the movement distance data (kurtosis = 6.5, $Z = 2.8$, $P = 0.005$; Fig. 1a) and the movement rate data (kurtosis = 7.0, $Z = 3.0$, $P = 0.002$; Fig. 1b). D’Agostino’s test for skewness revealed that movement distance data were negatively skewed (skew = -1.3 , $Z = -2.6$, $P = 0.009$) while movement rate data were positively skewed (skew = 1.5, $Z = 2.9$, $P = 0.003$). There was no difference in the distances fish moved upstream ($n = 11$) versus downstream ($n = 12$) based on the Mann-Whitney U test ($W = 76$, $P = 0.56$). There was no relationship between fish size (TL) and distance moved ($F_{1,21} = 0.39$, $P = 0.54$, $R^2 = 0.02$) or movement rate ($F_{1,21} = 3.12$, $P = 0.09$, $R^2 = 0.13$). Observed movement distances for the stationary (sigma-sta; 104.8 m) and mobile (sigma-mob; 608.9 m)

components of the *F. zebrinus* population were greater than expected movements generated with the R package ‘fishmove,’ which included a stationary estimate (95% interval) of 5.3 m (1.8–15.3) and mobile estimate (95% interval) of 94.5 m (41.5–215.5). Observed movement rate for the stationary component (8.5 m/day) was greater than the expected estimate of 1.6 m/day (0.5–5.5), but the observed rate for the mobile component (41.7 m/day) was within the 95% confidence interval of the expected estimate of 19.7 m/day (7.5–52.3). The share of the stationary component (p) for the observed movement distances was 0.80 and for the observed movement rates was 0.47.

Restricted movement by *F. zebrinus* was consistent or greater compared with other members of the genus *Fundulus*. Alldredge et al. (2011) studied the movement rates of *Fundulus notatus* in a fourth-order stream in Illinois and *Fundulus olivaceus* in a third-order stream in Mississippi, and Radinger and Wolter (2014) analyzed the data to estimate movement rates for stationary and mobile components for both species. The observed movement rates of *F. zebrinus* (8.5 m/day stationary; 41.7 m/day mobile) were comparable to *F. notatus* (5.9 m/day stationary; 42.4 m/day mobile) but greater than *F. olivaceus* (0.6 m/day stationary; 2.7 m/day mobile). In another study by Lotrich (1975), summer-time movement distances by *Fundulus heteroclitus heteroclitus* were tracked in a first-order stream in Delaware. When analyzed by Radinger and Wolter (2014), movement estimates for *F. h. heteroclitus* were 1 m (stationary) and 9.6 m (mobile) over a 52-day interval; these were much shorter distances compared with the 104.8-m (stationary) and 608.9-m (mobile) movements by *F. zebrinus* over an average time period of 17.5 days. Previous studies demonstrated sex-specific movements for *F. olivaceus* (e.g., Clark and Schaefer, 2016; Clark et al., 2019) and *F. heteroclitus* (e.g., Fritz et al., 1975) and although we did not collect data on sex, future research should address this point for *F. zebrinus*. When viewed collectively, these data support the notion that stream fish movement increases with stream size and that *Fundulus* fishes are generally restricted in their movement behavior (Radinger and Wolter, 2014).

Our study contributes to a greater understanding of the linkages between fish life histories and movement behaviors. Specifically, we provide quantitative movement information from the same region as a recent and comprehensive assessment of *F. zebrinus* life history (Ruppel and Bonner, 2020). Although our sample size was limited, our analysis of 23 recaptured individuals is comparable to previous movement studies (Skalski and Gilliam, 2000; Petty and Grossman, 2004; Wells et al., 2017). More broadly, our work provides quantitative support for previous assumptions that life history and movement by *F. zebrinus* contrast that of PBS fishes (Chase et al., 2015). Broader application of otolith microchem-

istry studies for PBS fishes in which *F. zebrinus* is used to approximate local water chemistry dynamics (sensu Chase et al., 2015) is needed in southern Great Plains streams where *F. zebrinus* is common and PBS fishes are in need of conservation and research attention (Perkin et al., 2015; Worthington et al., 2018). Our data support the use of *F. zebrinus* as a stationary species against which broad-scale movements (e.g., hundreds of kilometers) can be contrasted, but we also note that fine-scale movements (e.g., hundreds of meters) are slightly greater than predicted using recently developed RMP models (e.g., Radinger and Wolter, 2014).

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