



## Research

**Cite this article:** Blanchard RC, Perkin JS. 2026 Assessing movement patterns of the highly invasive western mosquitofish (*Gambusia affinis*). *Proc. R. Soc. B* **293**: 20251954. <https://doi.org/10.1098/rspb.2025.1954>

Received: 31 July 2025

Accepted: 11 November 2025

**Subject Category:**

Ecology

**Subject Area:**

ecology

**Keywords:**

aquatic invasive species, dispersal, movement, predicting invasion, restricted movement paradigm

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.8195034>.

# Assessing movement patterns of the highly invasive western mosquitofish (*Gambusia affinis*)

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RCB, 0009-0001-7558-2223

The western mosquitofish is among the top 100 invaders in the world, yet it continues to be introduced globally for mosquito control. This study investigates the movement patterns of the western mosquitofish and develops movement predictions for their continued invasion. We combined mark–recapture experiments, meta-analysis of previous movement studies and application of an existing fish movement model involving fish morphology, stream order and time to advance knowledge of western mosquitofish secondary spread. Our results reveal that small-scale and short-term movements by invasive western mosquitofish are predictable using existing statistical models. However, movement over larger scales and longer timelines was consistently underpredicted by existing models, suggesting our current understanding of invasion capacity by western mosquitofish is limited. We used sensitivity and optimization methods to identify parameter adjustments that make existing statistical models relevant for broader-scale invasions, and we illustrate the improved inference gained from this approach by modelling future spread of a recently invaded region. Our results provide quantitative estimates of western mosquitofish invasion across a range of contexts and can direct conservation and management actions aimed at improving invasion monitoring, predicting risk of secondary spread and understanding invasion dynamics at multiple spatiotemporal scales.

## 1. Introduction

Humans have been utilizing animals for biological control for thousands of years, with the first documented case dating back to around 2000 BC in Egypt, where cats were utilized to protect grain storage [1–4]. The first documented cases of fish being utilized for biological control dates back to the early 1900s, with the use of western mosquitofish, *Gambusia affinis* (Baird & Girard, 1853), and eastern mosquitofish, *Gambusia holbrooki* (Girard, 1859), to control mosquito populations [5,6]. The history of mosquitofish introduction is tied closely with the discovery that diseases such as malaria and yellow fever are spread by mosquitoes [7–9]. These discoveries were quickly followed by the introduction of mosquito control methods, including draining and drying standing water and utilizing species of fishes to control mosquito populations [10–12]. The mosquitofish was identified as a control agent, and domestic and international introductions began shortly after [5,6,13–16].

Until the late 1980s, the western and eastern mosquitofish were considered the same species, and therefore were not differentiated during the initial introductions, ultimately leading to both species being introduced interchangeably. Both mosquitofish species are part of the family Poeciliidae and are similar morphologically. The western and eastern mosquitofish differ by dorsal (6 versus 7 rays) and anal fin (9 versus 10 rays) ray counts as

well as gonopodium morphology (eastern having prominent teeth [17]). Both species have similar diets, primarily feeding on zooplankton, small insects and detritus [18,19]. Following their split from one species into two, improved resolution on their current distributions emerged. The eastern mosquitofish has a small native range, including the southeastern United States, from Florida to New Jersey, and as far inland as Alabama and Tennessee [20]. Their non-native range includes additional states in the continental United States, Puerto Rico and at least 20 countries [17,20]. The western mosquitofish has a larger native range, including the Mississippi River basin, from Central Indiana south to the Gulf, including Texas, and regions of northern Mexico [19]. Their invasive range encompasses at least 40 US states, both Puerto Rico and Guam, and over 75 countries. Consequently, western mosquitofish are believed to be the most widely disseminated predator in the history of biological control [5,21–23]. The western mosquitofish has been identified by IUCN as one of the 100 worst invasive species [24]. Given their extensive invaded range, the focus of this study is on the western mosquitofish. These fish can survive within a wide range of conditions, including hypersaline environments, a 40°C range in water temperature, pH ranging from 4.7 to 10.2 and dissolved oxygen levels as low as 0.5 mg l<sup>-1</sup> [25–27]. Their wide range of tolerances, as well as their ability to survive with a wide range of predators, have allowed them to invade diverse habitats following their introduction for mosquito control.

Roughly 50 years after their first introduction, research began into the detrimental impact that the western mosquitofish can have on the waterbodies where they are introduced. Detrimental impacts of the introduction of the species include declines in populations of native fishes, frogs and invertebrates, as well as destruction of habitats [5,13,22]. By 1958, the western mosquitofish (nicknamed the ‘fish destroyer’) was noted as an invasive species, and countries started banning their introduction [28–30]. Although numerous papers and articles have addressed the damages caused by introducing these fish, they continue to be distributed by government entities across the United States [31]. Perhaps the most startling discovery following their mass introduction was that initial studies may have exaggerated the reputation of the fish for its mosquito-eating ability, and that other, native species may consume just as many, if not more, mosquito larvae [5,32]. Given the detrimental impacts of their introduction coupled with overstated usefulness as vector control agents, a more mechanistic understanding of factors influencing western mosquitofish movement will benefit conservation and management actions.

Assessment of future spread of western mosquitofish requires insight into fish movement. Early studies described fish movement as largely restricted, hypothesizing that fish were sedentary with individuals living most of their lives in restricted home ranges despite their potential for longer-distance dispersal [33–35]. This idea, termed the restricted movement paradigm (RMP), became the major theory used to describe fish movement [35]. However, further research has revealed that most stream fish populations are heterogenous in their movement patterns, characterized by a large stationary component and a smaller mobile component [33,35,36]. The proportion of mobile fishes varies among species, but on average comprises 33% of the population [30]. The mobile components of fish populations are responsible for individual exchange among populations, dispersal and colonization (or recolonization) of habitats, making them the driving force of invasions [37]. Fish movement is considered leptokurtic, meaning that movement within a fish population can be represented as a distribution with a large peak at or near zero (the stationary component) and smaller peak with longer tails at large values (the mobile component), which contrasts with the shape of a classic normal distribution [31]. Modern fish dispersal models rely on the assumption of leptokurtic movement distributions, with fish populations comprised mobile and stationary components [30,31].

Identifying morphological and environmental conditions that allow for successful invasions is crucial, especially when predicting future invasions [38,39]. Prior studies have focused on morphologies that increase dispersal capabilities, with many identifying total length (TL) and caudal fin aspect ratio (ARC) as leading traits correlated with dispersal [30,40,41]. It is widely accepted that an increased TL is associated with an increase in dispersal distance [30,40,41]. ARC, which is defined as caudal fin height squared divided by caudal fin area, is positively correlated with stream fish dispersal capabilities [30,41,42]. Additionally, environmental factors, such as stream order, play a role in the spread of invasive species. Specifically, fish move farther in larger order streams, and it is generally accepted that dispersal distances are positively correlated with stream order [30,43,44].

The application and refinement of newer models of fish movement might advance our understanding of western mosquitofish invasion and secondary spread. The fish movement model developed by Radinger & Wolter [30] was used in this study to estimate expected fish dispersal distances. This model [36] is based on a meta-analysis of movement data from 62 stream fish species and identified predictors of movement magnitude. The four predictors utilized in this model include fish size (mm), stream order, time (days the fish are at large) and fish ARC [30,39]. The model estimates both expected dispersal distance and the proportion of mobile versus stationary individuals within a population. This framework allows for predicting fish movement across varying stream sizes and temporal scales. Independent studies have tested and validated this model using a variety of species, including banded sculpin (*Cottus carolinae*), plains killifish (*Fundulus zebrinus*) and prairie chub (*Macrhybopsis australis*) [40–42]. Although numerous studies have tested and validated this model, additional testing of the model on small-bodied fishes that were not included in the meta-analysis (i.e. western mosquitofish was not included) is needed to determine if this model can accurately predict the movement patterns of small fishes in both small and large rivers [45,46].

In this study, we explore movement patterns of the highly invasive western mosquitofish and apply this information to managing existing and future invasions. Additionally, we aim to broaden the scope of the Radinger & Wolter [30] model by testing its applicability on a small-bodied fish that was not included in the original meta-analysis. To do this, we developed four objectives. Our first objective was to assess movement patterns of the western mosquitofish in two first order streams using mark–recapture methods. Our second objective was to assess the applicability of the Radinger & Wolter [30] model as a predictor of fish movement through comparison of expected movement predicted by the model and field data collected from the mark–recapture study. Our third objective was to apply the movement model to previously published datasets to assess its accuracy in predicting mosquitofish movement across diverse habitats and scales. Our fourth and final objective was to demonstrate application of the model to a newly documented invasion and describe how it might be used to guide management and conservation actions.

## 2. Methods

### (a) Mark–recapture study

We assessed movement of western mosquitofish using four mark–recapture experiments spanning a six month period from March to August 2024. We selected two unconnected first order urban streams within the native range of the species, in Brazos County, Texas (figure 1). Both streams were selected due to the consistent presence of a mosquitofish population and at least a 300 m stretch of stream that was passible for small-bodied fishes. Additionally, these streams both are in highly urbanized areas, representing small urban streams that these fish are commonly introduced into for mosquito control. The selected streams differed in length, depth, flow and presence of additional species of fishes. The first stream, Hensel Creek, is a first order stream flowing in a residential area of College Station, Texas. Hensel Creek has a drainage area of 1.09 km<sup>2</sup> and is narrow, shallow and lacks flow except in times of high rain flow. The stream exhibits low species diversity, with populations of western mosquitofish and green sunfish present [47]. The second stream, White Creek (also a first order stream), flows through the Texas A&M University campus in College Station, Texas. White Creek has a drainage area of 3.33 km<sup>2</sup> and varies along its length in depth and width, with both flowing and non-flowing areas due to elevation change. White Creek additionally has higher species diversity with green sunfish, longear sunfish, red shiner, blacktail shiner, largemouth bass and channel catfish found in the creek in addition to the population of western mosquitofish [48]. The two selected streams were unconnected to each other, separated by natural and man-made barriers that ensured cross-site dispersal was not possible.

We conducted mark–recapture studies at both sites in both the spring and summer seasons of 2024. At each stream, a 280 m reach was identified and divided into seven 40 m subreaches for tagging. Each subreach was sampled using seines, and fish were transported in buckets to the bank of the stream for tagging using visible implant elastomer (VIE). Any western mosquitofish under 25 mm TL was returned to the stream due to size-based mortality of VIE tagging. Using a combination of four body locations and four colours of VIE, 16 combinations of tags were used, allowing us to differentiate where in the stream, as well as during which season the fish was tagged. Four tagging events took place, one at each site for both the spring and summer season. Mosquitofish were sexed, batch tagged according to subreach and allowed to acclimate in a bucket after tagging. Colour and body location of VIE tag for each subreach was noted, and fish were released into the centre of their collection subreach. Global positioning system (GPS) coordinates of the release point were noted for each subreach. Following tagging events, recapture events took place every two weeks for eight weeks. During recapture events, the entire 300 m reach of stream was seined to search for tagged individuals. We continued seining beyond the 300 m reach until potential barriers (road crossing culverts) were reached (10 m upstream 50 m downstream in Hensel Creek, and 10 m downstream and 200 m upstream in White Creek). After each seine haul, all fish were counted and visually inspected for a VIE tag. Non-tagged fish were released, and recaptured fish were placed into buckets according to seine haul number. Recapture location GPS coordinates were taken in the centre of each recapture seine haul. During the summer recapture events, fish were visually inspected for VIE tags injected during both the spring and summer tagging events. All recaptured fish were transported to Texas A&M University and euthanized using clove oil according to approved procedures (see ‘Ethics’ below for further details). For each recaptured fish, TL and ARC were calculated. Both TL and the measurements required to calculate ARC (caudal fin height and area) were measured from individual photos taken of recaptured fish. All GPS data and morphological features were read into R (v. 4.4.1) for analyses [49].

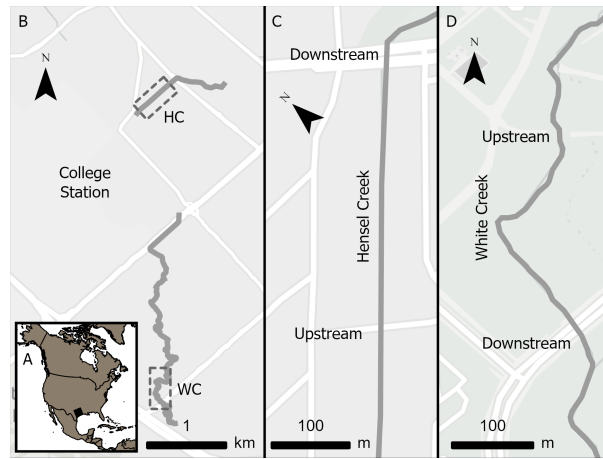
For each recaptured fish, the distance and direction moved were calculated using the ‘riverdist’ package [50]. This approach required uploading mark and recapture locations as well as a stream shapefile over which total displacement (i.e. distance moved along the streamline) could be calculated. We used the National Hydrography Dataset High Resolution version stream polylines [51] to represent the stream over which distances were measured. Rate of movement (m d<sup>-1</sup>) was calculated by dividing the total distance moved (m) by the number of days between tagging and recapture events for each fish. We tested for the general pattern of fish movement using the Anscombe–Glynn test of Kurtosis from the ‘moments’ package [52]. This analysis assigns a kurtosis value to the data, with a value of 3 representing a mesokurtic distribution and a value above 3 representing a leptokurtic distribution. We tested for upstream or downstream bias of fish movement using the Wilcoxon test from the ‘stats’ package [49]. Additionally, we tested for skewness in fish movement using the D’Agostino test of skewness from the ‘moments’ package [52]. All tests were run independently for each season and site, as well as with a combined dataset of all recaptured fish.

### (b) Validation of the fish movement model

We tested if mosquitofish moved farther than expected under the RMP using the ‘fishmove’ package [30]. To do this, we first estimated movement of our recaptured fish using the ‘fishmove.estimate’ function, which estimates the average distance moved (m) for both the mobile and stationary components of the recaptured fish population. Estimation of movement distances was based on the distance ( $x$ ) from the tagging location using the equation

$$F(x) = p \times \frac{1}{\sqrt{2\pi\sigma_{\text{stat}}^2}} \times e^{-\frac{(x-\mu)^2}{2\sigma_{\text{stat}}^2}} + (1-p) \times \frac{1}{\sqrt{2\pi\sigma_{\text{mob}}^2}} \times e^{-\frac{(x-\mu)^2}{2\sigma_{\text{mob}}^2}}, \quad (2.1)$$

where  $p$  was equal to the share of the stationary component of the total population,  $\sigma_{\text{mob}}$  was equal to the mean movement distance of the mobile component and  $\sigma_{\text{stat}}$  was equal to the mean movement distance of the stationary component [30]. The ‘fishmove.estimate’ function uses optimization to solve for  $\sigma_{\text{stat}}$  by estimating the standard deviation of the first distribution,



**Figure 1.** Study area for western mosquitofish mark–recapture experiment showing (A) the study location within North America (black diamond) and (B) College Station, TX, with dashed boxes showing the relative locations of (C) Hensel Creek and (D) White Creek. Streams are shown as dark grey, and roads are shown as white.

$\sigma_{\text{mob}}$  as the standard deviation of the second distribution and  $p$  as the weighing factor for the distributions. This model assumes a symmetrical dispersal kernel and only uses absolute movement distances (i.e. negative sign used to denote downstream movement is not included in the model). We estimated fish movement for each recapture event independently. Additionally, we calculated a 95% confidence interval for our observed fish movement using the outputs of the ‘fishmove.estimate’ function, which included average distance moved and standard error. We then predicted the average movement of fish in the mobile and stationary components of a hypothetical population using the ‘fishmove’ function. Estimation of the movement distance by the stationary component were derived from a multiple linear regression model originally published by Radinger & Wolter [30] using the equation

$$\log(\sigma_{\text{stat}}) = -10.57 + 1.64 \log(L) + 0.97(\text{AR}) + 1.14 (\text{SO}^{0.5}) + 0.43 \log(T), \quad (2.2)$$

while estimation of the movement distance by the mobile component were derived using the equation

$$\log(\sigma_{\text{mob}}) = -7.48 + 1.45 \log(L) + 0.58(\text{AR}) + 1.51 (\text{SO}^{0.5}) + 0.55 \log(T), \quad (2.3)$$

where  $L$  was fish total length (mm), AR was caudal fin aspect ratio, SO was stream order,  $T$  was time between mark and recapture (days) and  $\log$  represents the natural logarithm. Time at large (number of days between tagging event and recapture event) varied for each prediction, and we used the total number of days between tagging and recapture events for each recapture event. For TL and fin morphology, we used the average TL (mm) and average ARC of the recaptured fish at any given recapture event. Stream order was set to 1st order for all predictions for Hensel and White creeks. We predicted fish movement for each recapture event independently. To this end, we created a total of 20 predictions (Hensel Creek Spring = 8 predictions, White Creek Spring = 5, Hensel Creek Summer = 4 and White Creek Summer = 3). For each prediction, the average distance moved ( $\pm 95\%$  confidence intervals) by the mobile and stationary components were estimated. To determine if fish moved farther than expected under the model, observed fish movement was compared to expected movement predicted by the model.

We used two additional case studies to validate the Radinger & Wolter [30] fish movement model. These case studies allowed us to test the validity of the model for predicting the movement of western mosquitofish in a small man-made system and in larger-order rivers. The first case study was based on Cote *et al.* [53], which investigated the relationship between personality traits and dispersal tendencies of the western mosquitofish in a small man-made system that mimics water troughs that mosquitofish are commonly stocked in for mosquito control [53]. The case study dataset included the number of fish, distance moved by each fish and the amount of time the fish were given to move throughout the mesocosm. These data were coupled with the average fish size (42.45 mm TL) and ARC ratio (1.40) from our mark–recapture data to predict movement. We used raw movement distance data from Cote *et al.* [53] to estimate observed fish movement using the ‘fishmove.estimate’ function as describe above, and a combination of our data (TL, ARC) and Cote *et al.* [53] data (time at large, stream order) to estimate expected fish movement using the ‘fishmove’ function as described above. Because the mesocosm experiment by Cote *et al.* [53] was conducted for 24 h, we set time at large to 1 day and stream order to 1st order. We then compared the observed and expected results to test the validity of the predictive model in a small, man-made system.

The second case study was based on Lynch [54], which followed the non-native introduction and secondary spread (presumably via dispersal) of western mosquitofish across three river systems in Nebraska (The South Platte, Republican and Elkhorn Rivers). Data from Lynch [54] included distance travelled by the mosquitofish population (km) and the years at which the fish were first identified in various stretches throughout the river in both upstream and downstream directions from the first occurrence. We coupled data from the case study with data from our mark–recapture study to develop observed and predicted movement distances by western mosquitofish using the ‘fishmove.estimate’ and ‘fishmove’ functions as described above. For the predictions, time was set to the number of days between estimated introduction and new occurrences listed by Lynch [54]. We utilized the average fish size (42.45 mm TL) and ARC ratio (1.40) from all fish we recaptured in the field. Stream order was obtained for each river using the National Hydrography Dataset [51]: Elkhorn River (5th order), Republican River (6th order)

**Table 1.** Number of fish tagged and recaptured as well as movement and size statistics for each site and season included in the mark–recapture study. Values include the mean and range (in parentheses).

	Hensel Creek spring	White Creek spring	Hensel Creek summer	White Creek summer	total
fish tagged	463	101	1002	99	1665
fish recaptured	207	19	217	25	468
percentage recaptured	45	19	22	25	28
mean distance moved (m)	23.6 (0–264.9)	40.8 (0–207.7)	11.7 (0–172.7)	33.3 (0–128.5)	19.6 (0–264.9)
mean time at large (day)	28.4	29.6	18.6	21.8	23.4
mean movement rate (m day <sup>-1</sup> )	0.95	2.09	0.57	1.95	0.89
mean total length (mm)	41.0	46.3	43.4	44.8	42.4
proportion stationary	0.37	0.48	0.59	0.44	0.47

and the South Platte River (7th order). We compared observed and expected distances to determine if the model accurately predicted fish movement in these rivers.

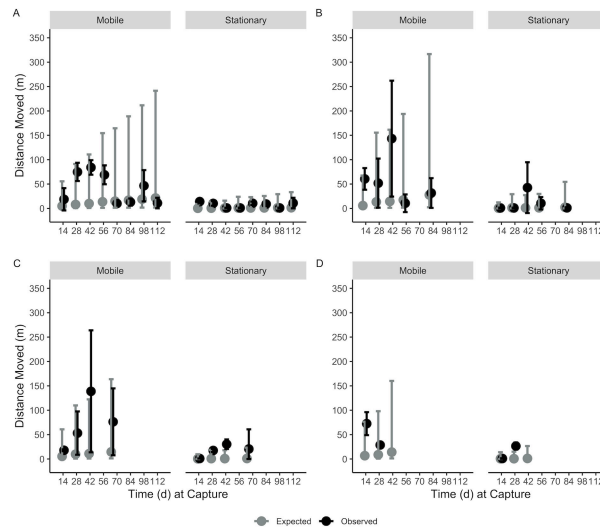
We combined results from our mark–recapture study with the two case studies [48,49] to generate a dataset of observed versus predicted movement distances by the mobile component of western mosquitofish populations. We focused on the mobile component because this component is responsible for secondary spread via dispersal [55]. The compiled dataset had 32 observations of predicted versus observed movements, including one observation from Cote *et al.* [53], 20 observations from our mark–recapture experiment and 11 observations from Lynch *et al.* [54]. We first assessed agreement between observed movement and predicted movement using the standard model of Radinger & Wolter ([30]; equation (2.3)) as described above. We quantified ‘agreement’ using the slope of the relationship between observed (*x*-axis) and predicted (*y*-axis) movement distances. A slope equal to 1 would represent consistent scaling for observed versus predicted movements, while a slope value <1 would represent under-prediction by the model (i.e. fish were observed to move farther than the model predicted). Our initial results were consistent with earlier work suggesting small fish might move farther over a shorter amount of time in large rivers than the model predicts [41]. Consequently, we developed a sensitivity analysis to explore the effects of augmenting predictive linear model parameter values (i.e. slopes in equation (2.3)) for stream order and time by up to 300%. This sensitivity analysis assessed the level of agreement for the relationship between observed and predicted movement (measured by the slope of that relationship) across 100 values for the stream order parameter (from 1.51 to 4.50 by 0.03 increments) and across 100 values for the time parameter (from 0.55 to 1.54 by 0.01 increments). We fit predictions for every combination of stream order and time parameter values (10 000 iterations) and calculated the slope and correlation coefficient of the relationship between observed and predicted for each iteration to reveal the identity and magnitudes of parameter value adjustments that best described the relationship between observed and predicted western mosquitofish movement.

### (c) Application of the fish movement model and its adjustments

We applied the standard and adjusted western mosquitofish movement model to a recent introduction of western mosquitofish into the Eastern Himalayas, China. Wang *et al.* [56] detailed the introduction of mosquitofish into China and reported the location, number of fish, photographs and measurements of individuals [56]. We used these data to illustrate how predictions from various iterations of the model could be used to inform monitoring and management. We predicted movement over a 10 year window (3652.5 days) from a hypothetical introduction point at a road-stream crossing near the documented occurrence published by Wang *et al.* [56]. We developed predictions using TL (31 mm) and ARC (1.08) estimated from photographs reported by Wang *et al.* [56]. Stream order for waterways was obtained using the Hydrosheds database. Two points of note for these projections are that (1) they assume that fish will move, or be moved from a lentic system to a nearby lotic system [57,58] and (2) dispersal is predicted over multiple generations of western mosquitofish rather than by individuals over a short time period. We developed predictions for each of the four scenarios of the model described above, including the standard model, a model with only stream order augmented, a model with only time augmented, and a model with stream order and time jointly augmented.

## 3. Results

We tagged a total of 1665 western mosquitofish across four mark–recapture events on Hensel Creek and White Creek (table 1). The majority were tagged at Hensel Creek (spring = 463, summer = 1002) with fewer tagged at White Creek (spring = 101, summer = 99). Of the 1665 fish tagged, 468 were recaptured (28% recapture rate). Of the 468 recaptured fish, 19 were recaptured during the summer that had been tagged during the spring (Hensel Creek = 17, White Creek = 2). Fish moved farther on average, both in total distance and rate per day, in White Creek compared with Hensel Creek. The proportion of the recaptured fish considered stationary differed across mark–recapture events and study systems. Mosquitofish movement distance and rate were generally classified as leptokurtic and were positively skewed in an upstream direction when site and season movement data were combined. When considered individually, exceptions to this pattern included White Creek during the summer of



**Figure 2.** Mean (points) and 95% confidence intervals (lines) illustrating strong agreement between observed (black points and lines; based on mark–recapture) and expected (grey points and lines; based on empirical modelling) movement of western mosquitofish. Mobile (left panels) and stationary (right panels) movement distances are shown for time series mark–recapture events in (A) Hensel Creek in spring, (B) White Creek in spring, (C) Hensel Creek in summer and (D) White Creek in summer. See electronic supplementary material, table S2, for details on distances moved.

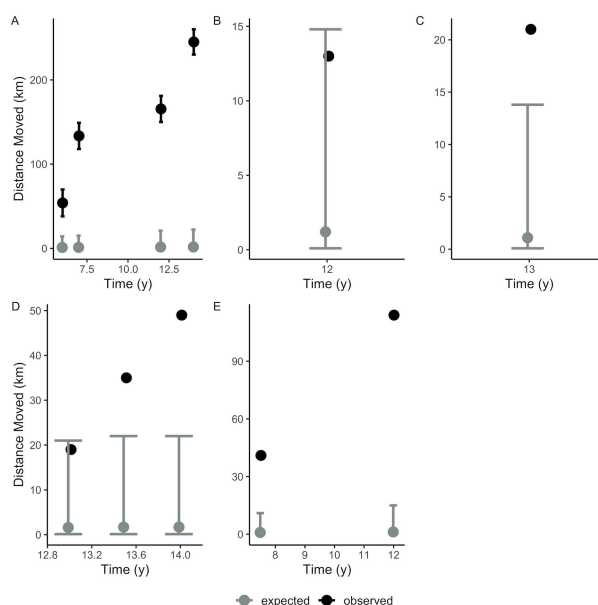
2024 when movement distance was mesokurtic and non-skewed (electronic supplementary materials, figure S1 and table S1). Violin plots (electronic supplementary material, figure S2) illustrated unequal distributions of distances moved upstream and downstream.

Observed western mosquitofish movement derived from mark–recapture methodology was consistent with model predictions (figure 2; electronic supplementary material, table S2). The expected movement distances differed between seasons and sites, with the farthest expected movement for White Creek in the spring. Observed movement distances had overlapping confidence intervals with expected movement for all time points in Hensel Creek in spring (figure 2A) and White Creek in the spring (figure 2B). Only one incidence of non-overlapping confidence intervals occurred for Hensel Creek in the summer (at day 40 the stationary component moved farther than expected; figure 2C) and one for White Creek in the summer (at day 28 where the stationary component moved farther than expected; figure 2D). Despite the general overlap between expected and observed movements, we noted that point estimates of observed movement magnitudes were generally greater than expectations from the model.

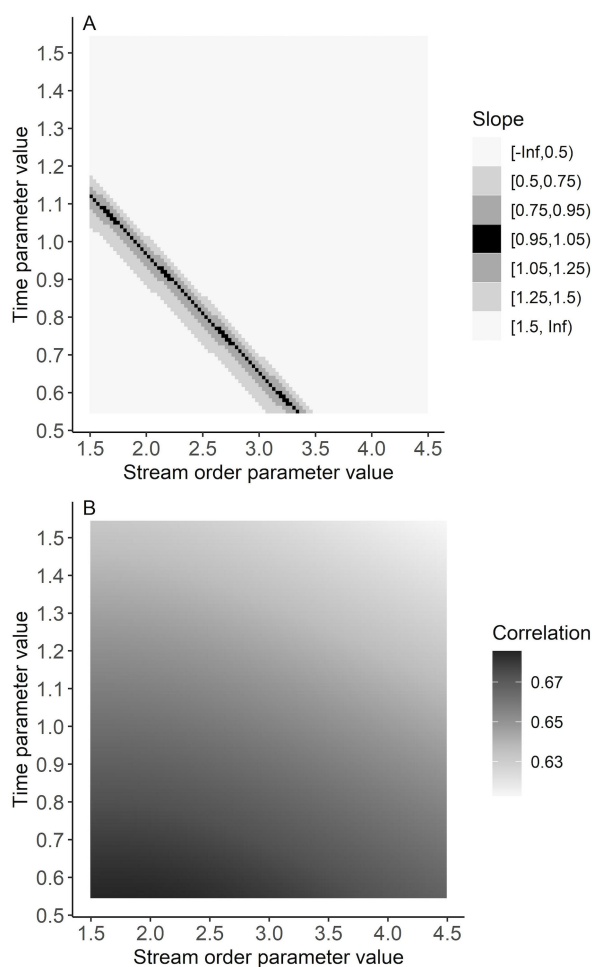
Validation of the Radinger & Wolter [30] fish movement model using previously published studies illustrated high accuracy over shorter durations, but an attenuation of accuracy caused by greater observed movements relative to expected movements as scales increased. When applied to the Cote *et al.* [53] data, the fish movement model accurately predicted expected mosquitofish movement over a day in small man-made habitats (electronic supplementary material, figure S3). Once again, although confidence intervals overlapped, we noted that observed movement estimates were larger than those predicted by the model. In Nebraska rivers, where the mobile component of western mosquitofish was tracked through its invasion of three rivers, there was a decrease in the accuracy of the fish movement model, particularly in larger streams over longer time periods. The model underestimated fish movement by over 200 km in downstream movement in the South Platte River (figure 3A). The model did accurately predict movement distances for downstream movement in the Republican River (figure 3B), although we note that fish movement was restricted due to the presence of Harlan County Lake, 13 km downstream. The model also underestimated downstream movement in the Elkhorn River by over 5 km (figure 3C). The model underestimated movement upstream for both the South Platte (figure 3D) and Republican (figure 3E) rivers by as much as 75 km, although it did have success at the 13 year upstream movement prediction in the South Platte River.

Sensitivity analysis revealed parameter value adjustments that maximized agreement between observed and predicted movement. Across the 10 000 iterations, there was evidence for strong agreement (i.e. slope = 1) between observed and predicted movement across a narrow band of parameter values (figure 4A), despite correlation coefficients remaining within 0.61–0.69 across the range of iterations (figure 4B). The standard model parameter values resulted in underprediction of longer distance movements characterized by slope = 0.008 and  $r = 0.69$  (figure 5A). Adjustment of only the stream order parameter from 1.51 to 3.34 (while holding time at 0.55) yielded a slope = 1.02 and  $r = 0.68$  (figure 5B). Alternatively, adjusting the time parameter from 0.55 to 1.12 (while holding stream order at 1.51) yielded a slope = 0.99 and  $r = 0.66$  (figure 5C). The sensitivity analysis also revealed that smaller magnitude adjustments to both parameters (e.g. stream order from 1.51 to 2.44, time from 0.55 to 0.83) yielded slope = 1.00 and  $r = 0.67$  (figure 5D).

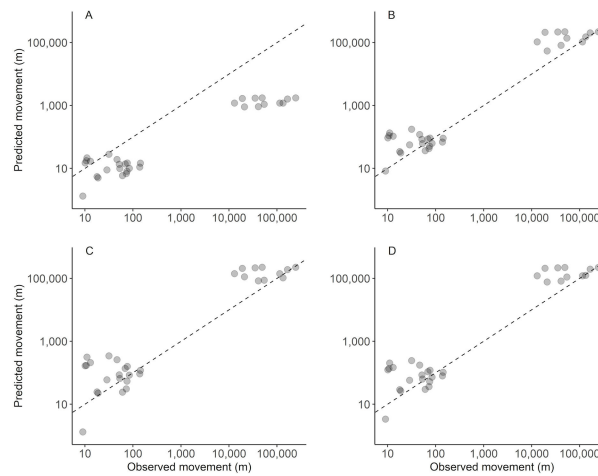
Application of the fish movement model and its adjustments illustrated how secondary spread of western mosquitofish in the Eastern Himalayas might occur. If introduced to the nearest stream at a road–stream crossing, western mosquitofish might move 63 m in upstream and downstream directions over a 10 year period under the standard movement model (figure 6A). Augmenting the stream order parameter of the standard model increased predicted movement to 394 m in upstream and downstream directions over a 10 year period (figure 6B). Augmenting the time parameter substantially increased predicted dispersal to include the entirety of the first-order streams, as well as 77 km in upstream and downstream directions of the nearby eighth-order mainstem Yarlung Tszango River over a 10-year period (figure 6C). Jointly augmenting the stream order



**Figure 3.** Mean (points) and 95% confidence intervals (lines) illustrating general disagreement between observed (black points and lines; based on population monitoring) and expected (grey points and lines; based on empirical modelling) movement by the mobile component of western mosquitofish populations in three large rivers studied by Lynch [54]. Only mobile component movement distances are shown for (A) downstream movement in the South Platte River, (B) downstream movement in Republican River, (C) downstream movement in the Elkhorn River, (D) upstream movement in the South Platte River and (E) upstream movement in the Republican River. Note that y-axis scales differ among panels.



**Figure 4.** Heatmaps illustrating results of sensitivity analysis for adjustments to slope parameter values in equation (2.3) to maximize agreement (i.e. slope value closest to 1) between observed and predicted movement. Heatmaps are based on 10 000 iterations in which all possible combinations of incremental increases in the parameter values for stream order and time were increased up to 300% of their original values. Darker colours for cells indicate stronger agreement for (A) change in slope and (B) change in correlation coefficients across iterations.



**Figure 5.** Scatter plots showing agreement between observed ( $x$ -axis) and predicted ( $y$ -axis) movement of the mobile component of western mosquitofish populations across studies and model implementations. Points are observations of movement, and the dashed line represents a 1 : 1 relationship between observed and predicted (i.e. a slope = 1). (A) The relationship based on the standard model of Radinger & Wolter [30] shown in equation (3). (B) The relationship after adjusting only the stream order parameter (from 1.51 to 3.34). (C) The relationship after adjusting only the time parameter (from 0.55 to 1.12). (D) The relationship after adjusting the stream order parameter (from 1.51 to 2.44) and the time parameter (from 0.55 to 0.83). Parameter value adjustments were selected to achieve a slope = 1 based on the output of the sensitivity analysis shown in figure 4.

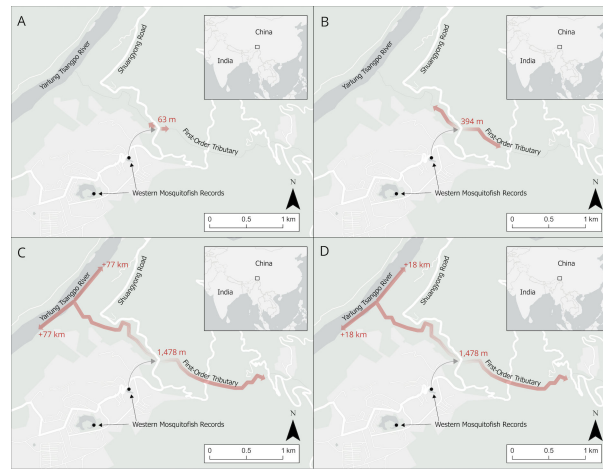
and time parameters increased predicted movement to include the entirety of the first order stream plus 18 km upstream and downstream in the mainstem Yarlung Tszango River (figure 6D).

## 4. Discussion

Through our mark–recapture study of western mosquitofish, we investigated movement patterns of this highly invasive species and integrated mosquitofish movement into current movement theory. First, we observed high recapture rates in both systems, recapturing nearly 30% of all tagged fish. Fish movement was observed to be generally leptokurtic, matching movement patterns typically observed in other fish species [30,59,60]. However, we observed a reduced proportion of stationary fish (i.e. 0.37–0.59) compared with typical values for other species (~0.67) [36]. Additionally, our study shows that the Radinger and Wolter fish movement model can accurately predict western mosquitofish movement in small 1st order rivers, as well as in small man-made mesocosms which are similar in size and depth to systems that the fish are introduced into for mosquito control. Although the model tested here accurately predicted small scale movement of western mosquitofish, the applicability to large order rivers was less accurate. In this study, we applied a fish movement model to mosquitofish movement across three larger order rivers across Nebraska, as published by Lynch [54]. We found that the model underestimated the distances moved by western mosquitofish as time increased, and as river order increased. Additionally, we created correctional values to augment movement predictions for western mosquitofish in large order rivers to more accurately predict their invasion following introduction into the Eastern Himalayas. Following the implementation of the augmented values into our predictions, the timeline for the opportunity to control invasion once they have been introduced shortens dramatically. These findings, coupled with the studies above, suggest that in large rivers, small-bodied fishes can rapidly disperse, moving much farther than current models predict.

The increased percent of western mosquitofish considered mobile has been noted previously, perhaps most importantly by Rehage & Sih [38], where they investigated the invasive tendencies of mosquitofish species. Their study noted an extremely high percentage of western mosquitofish being mobile, and they classified nearly 97% of western mosquitofish as mobile, also noting that the western mosquitofish disperse farther than non-invasive *Gambusia* species [38]. Given that the mobile component of a population is typically assumed to drive colonization and invasion, western mosquitofish having a large mobile component could contribute to their rapid secondary spread following global introductions [37]. Additionally, our mark–recapture data generated results consistent with other studies focusing on movement bias of fishes. Our study showed that upstream/downstream bias was dependent on system, as well as season. This may be attributed to water level changes, given high amounts of rain accumulation during the summer sampling season. Prior studies have noted that small-bodied fishes like the western mosquitofish are susceptible to downstream displacement during floods, which could explain the downstream bias noted in fish recaptured during the summer in Hensel Creek [61,62]. It must be stated, that although this model accounts for multiple variables, like morphology and stream size, it does not account for additional variables that could influence dispersal distances, including seasonal changes in water levels and flow, and behavioural differences. The addition of these variables to future movement models could improve the accuracy of predictions and allow the model to more accurately predict fish movement across a wider variety of scales.

The integration of movement data from small-bodied fishes into major movement models is vital, given that they are underrepresented in movement models, and studying movement of small-bodied fishes can be difficult [30,46,63]. Our results parallel other studies focusing on small fish movement in large rivers. Steffensmeier *et al.* [64] utilized the same



**Figure 6.** Maps depicting scenarios of potential spread of western mosquitofish over a 10 year period in the eastern Himalayas where Wang [50,56] recently reported occurrence of the species (black dots). In the event of movement from ponds into the closest stream where a road crosses (dark grey arrow), spread is modelled under (A) the standard movement model of Radinger & Wolter [30] in which case the species moves 63 m in upstream and downstream directions, (B) a model in which only the stream order parameter is augmented, (C) a model in which only the time parameter is augmented and (D) a model in which the stream order and time parameters are jointly augmented.

model to investigate movement patterns of prairie chub (*Macrhybopsis australis*; maximum TL 70 mm) in both 5th and 6th order streams. Their results show that fish were moving much farther than expected based on predictions made by the model [64]. Similar results were noted in red shiner (*Cyprinella lutrensis*; maximum TL 90 mm) and in Rio Grande silvery minnow (*Hybognathus amarus*; maximum TL 89 mm) in a 7th order river, with fish moving significantly farther than the model predicted [46,65]. This concept of large connective rivers acting as ‘super highways’ for invasive fish movement has also been studied in invasive fish species, including the grass carp (*Ctenopharyngodon idella*) and round gobies (*Neogobius melanostomus*) [58].

To best combat the continued invasion of the western mosquitofish, two major hurdles must be overcome. The first is focusing on local removal efforts of the species where they are already present, and the second is focusing on policy implementation ensuring that the species does not continue to be released into novel habitats. First, regarding controlling and eradicating local populations, it is important to consider the rapid rate of dispersal the fish are capable of in large rivers. Given this, conservation efforts might be more effective if geared towards eradication in small, isolated habitats, and ensuring that western mosquitofish or ecologically similar species are removed prior to reaching large rivers. Vander Zanden & Olden [66] focus on a similar concept, noting that in many instances, aquatic invasive species have established isolated populations, but have not yet spread to farther, more connected habitats. It is in these instances where conservation efforts are vital. There have been many proposed methods to slow the spread of already present invasive species, from gillnetting in small ponds and lakes, and electrofishing in larger streams and rivers [67]. It is important to note, though, that many of these proposed methods have proven ineffective or detrimental to native species and would be ill-advised when focusing on the western mosquitofish, given their small size. One proposed method for mosquitofish eradication is the temporary draining of freshwater habitats, which is ironic given that this same strategy was once suggested for mosquito control prior to widespread mosquitofish introductions [10,68]. A method of invasive species control that has been utilized to stop mosquitofish movement in the past involves placement of barriers (both physical and electric) [69–71]. The placement of barriers tends to have negative impacts on local species, so can be considered ineffective for slowing the spread of invasive species, however, given that the western mosquitofish is known to live in shallow, highly disturbed streams where other aquatic species cannot survive, physical fish barriers may be an effective control method, with little potential risk to native species. Artificial barrier placement has been utilized to quell mosquitofish movement previously, to aid in conservation of the redbfin blue eye (*Scaturiginichthys vermeilipinnis*) [71,72]. However, it is important to note that different techniques may be better suited for different sites, because habitat variability can influence mosquitofish survival and movement. Additionally, mosquitofish are known to have behavioural variation that influences their dispersal tendencies, which must be considered when selecting methods of population control. Because of this, multiple management techniques may be needed to use together to provide the best result for local mosquitofish eradication. Future research should be geared towards identification of effective methods to stop the spread of mosquitofish, and effectiveness of different removal techniques.

The second major hurdle to the goal of slowing or stopping the spread of the western mosquitofish is the fact these fish are still being introduced in many locations around the world. Policies have been put in place around the United States, mainly the Nonindigenous Aquatic Nuisance Prevention and Control Act (in 1990) with a goal of controlling the introduction of invasive species [69]. More specifically to mosquitofish, policies have been put in place in New Zealand, Australia, Canada and parts of the United States such as Minnesota and Wisconsin to stop their continued introduction [73–77]. However, the western mosquitofish continues to be introduced for mosquito control purposes, further aiding their current global invasion. Moving forward, ensuring that policy focusing on invasive species control is implemented regarding the western mosquitofish is vital. This study emphasizes that a two-pronged approach will be vital to stop mosquitofish invasions. Efforts need to be geared towards implementing legislature to stop their introduction, and local eradication in small, isolated habitats to prevent their

spread into larger habitats where they are likely to disperse extremely quickly. Our study provides guidance on the spatial and temporal scales that can be used to inform conservation decisions and ultimately slow mosquitofish invasion on a global scale. Specifically, knowledge gained from this study can be used in planning frameworks that seek to optimize the distribution of control efforts to match the pace of invasions [78], identify the spatial scales that should be included in models forecasting spread [66] and provide the necessary tools to scale invasion dynamics models down from the species level to specific locations and populations [79].

**Ethics.** Collection, care, use and euthanization of animals complied with approved Texas A&M University Animal Care and use Committee animal use protocol (2023-0308) and Texas Parks and Wildlife Scientific Collection Permit guidelines (permit SPR-0218-068).

**Data accessibility.** All data and code can be found in Dryad [80].

Supplementary material is available online [81].

**Declaration of AI use.** We have not used AI-assisted technologies in creating this article.

**Authors' contributions.** R.B.: data curation, formal analysis, methodology, writing—original draft; J.S.P.: conceptualization, formal analysis, supervision, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

**Funding.** This study was funded by the Tom Slick Research Fellowship awarded to Rose Blanchard by the Department of Ecology and Conservation Biology at Texas A&M University. Additionally, this work was funded by the US Army Corps of Engineers' Aquatic Nuisance Species Research Program's focus on Next Generation Ecological Modelling.

**Acknowledgements.** We thank the members of the Riverscape Ecology Lab for their help with collections of these specimens. We thank the members of the Paleoecology, Evolution and Climate lab for their support and help with statistical analyses.

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