

March of the sculpin: measuring and predicting short-term movement of banded sculpin *Cottus carolinae*

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Abstract – Movement of fishes through space and time is critical for population regulation and community structuring, but the dispersal of many benthic stream fishes remains unstudied. We used passive integrated transponders to track the short-term dispersal of 51 banded sculpin *Cottus carolinae* throughout a 600 m reach of Little Creek in central Tennessee during April and May. Our objectives were to assess the efficacy of recently developed dispersal models, evaluate temporal variability in movement and determine whether individuals switched between stationary and mobile movement behaviours. Observed movement distances did not differ from modelled leptokurtic dispersal kernels estimated using the *fishmove* package in the R Statistical Environment for 12 of 13 recapture occasions. Leptokurtic dispersal kernel parameters including the mobile component (σ_{mob}) and shared stationary component (p) were temporally dynamic and differed from static median values reported for fishes in *fishmove*, while the more abundant stationary component (σ_{stat}) showed agreement with *fishmove*. The recapture occasion during which model predictions were not validated was associated with a large flow pulse that stimulated increased movement at the population scale. At the individual scale, 28 of 51 fish switched between stationary and mobile dispersal behaviour and the frequency distribution of switches was leptokurtic. Collectively, our findings reveal an emergent property characterised by consistent upstream movement of banded sculpin despite variability in population-scale responses to flow and individual-scale switches in movement behaviour. This paradox represents the march of the sculpin, in which fish diffusively spread upstream at a constant rate despite multiscale variability in movement behaviours.

Key words: leptokurtic dispersal; restricted movement; mark–recapture; passive integrated transponders; *fishmove* package; *Cottus carolinae*

Introduction

Movement of fishes across aquatic landscapes is critical for population regulation, community structuring and ecosystem functioning (Taylor et al. 1993; Radinger & Wolter 2014). Concepts from early fish movement studies (Gerking 1953; Funk 1955) are now framed within broader landscape contexts to predict fish movement among spawning, refuge and feeding habitats (Schlosser 1991). On fine scales (10^1 – 10^2 m), fishes move to the most suitable habitat

to ensure optimum growth and survival (Hill & Grossman 1993; Gowan & Fausch 2002). At broader scales (10^3 – 10^5 m), fishes move to access spawning habitats, disperse between populations, colonise or recolonise unoccupied habitats, and move to new habitats based on life-history requirements (Wine-miller & Jepsen 1998; Jackson et al. 2001). However, the mechanistic underpinnings that drive movements and the spatiotemporal scales at which fishes move remain largely unknown for most species despite the implications these processes hold for conservation

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and management of stream fish diversity (Fausch et al. 2002; Cooke et al. 2012).

Established theoretical guidelines for the ecology of fish movement in freshwater environments suggest stationary and mobile components exist within populations. The theory of restricted movement, also called the restricted movement paradigm (RMP, Gowan et al. 1994), posits that mature stream fishes are stationary and spend most of their lives in 20–50 m reaches of stream (Gerking 1953, 1959). This paradigm has been applied to characterise movements of fishes, although it is not applicable to all fishes (Penczak 2006). For example, 12–33% of individuals across four species in an Ouachita Highland stream were captured outside of habitats in which they were marked (Smithson & Johnston 1999), challenging the notion that fishes remain entirely stationary. One of the first studies to formally challenge the RMP used resident salmonids as an example to suggest designs of studies supporting the RMP involved bias against detection of movements outside of focal habitats (Gowan et al. 1994). More contemporary adjustments to the RMP suggest movements out of focal habitats (displacement) can be short or restricted but still sufficient to cause turnover (replacement of marked fishes by unmarked fishes; Rodríguez 2002). Turnover is driven by stationary and mobile contingents within populations (Rodríguez 2002) and is best predicted by leptokurtic dispersal models that capture the diffusive spread of ‘fast fish’ and ‘slow fish’ across aquatic landscapes (Skalski & Gilliam 2000). Heterogeneous models such as leptokurtic dispersal models differ from normal distributions because of higher peaks associated with large numbers of stationary fish and longer tails associated with small numbers of mobile fish dispersing longer distances (Skalski & Gilliam 2000). In a review of 62 species of fish, Radinger & Wolter (2014) found that leptokurtic dispersal models best-estimated fish movement regardless of movement distance and that the stationary component (66% of individuals) was larger than the mobile component (34% of individuals). This unifying theme of fish movement was recently developed into a modelling tool useful for predicting fish movements based on known swimming-related morphology, stream size and timescales (Radinger et al. 2014; Radinger & Wolter 2015). These theoretical advances and newly developed modelling frameworks fill a gap in research related to stream fish movement by allowing for the estimation of dispersal for unstudied fishes. However, validation of these models is currently lacking for benthic stream fishes whose movements have generally not been studied (Petty & Grossman 2004; Hudy & Shiflet 2009; Day et al. 2016).

Within the habitat guild of benthic stream fishes, movement of species within the genus *Cottus* has received increased attention in recent years. Movement patterns of mottled sculpin *Cottus bairdii* are most widely studied among freshwater sculpins with studies tracking movements in streams in Montana (McCleave 1964; Brown & Downhower 1982), North Carolina (Hill & Grossman 1987; Petty & Grossman 2004) and Michigan (Breen et al. 2009; Deboer et al. 2015). These studies collectively show stationary and mobile components exist within populations distributed across a broad geographic range and across a gradient of streams ranging from first to fourth order (Strahler 1957; Hudy & Shiflet 2009). Movement by banded sculpin *Cottus carolinae* is undocumented beyond a single study suggesting members of the species reside within a 6 m stream reach during their lifetime (Greenberg & Holtzman 1987). Current knowledge of banded sculpin movement is reflective of early understanding of fish movements when ‘restricted movement’ was first coined (Gerking 1953, 1959), and it stands to reason that a mobile component might exist in addition to the already-documented stationary component reported by Greenberg & Holtzman (1987). Furthermore, it remains unclear whether *Cottus* fishes are capable of switching between stationary and mobile behaviour within short time periods or within a single season (Petty & Grossman 2004). Switching of dispersal behaviour has strong implications for population regulation and responses by fish to environmental alterations (Crook 2004) and might be addressed by applying passive integrated transponder (PIT) technology to monitor individual fish dispersal histories (Roussel et al. 2000; Ruetz et al. 2006).

The goal of this study was to measure short-term dispersal of banded sculpin in Little Creek, Tennessee, to assess the applicability of recently developed predictive dispersal models and test for temporal variability in movement. Specific objectives included the following: (i) assess the validity of morphology-based predictive dispersal models; (ii) measure temporal variability in sculpin movement within a single season and relate movement to fish size, stream discharge and water temperature; and (iii) test for switching behaviour in which individual sculpin transition between stationary and mobile movement. We hypothesised that banded sculpin movement would conform to a leptokurtic dispersal model characterised by ~66% of individuals remaining stationary and ~34% of individuals expressing mobility (Radinger & Wolter 2014). We also hypothesised that temporal variation in sculpin movement would result in switching between stationary and mobile movement behaviours for individual fish (Petty & Grossman 2004; Deboer et al. 2015).

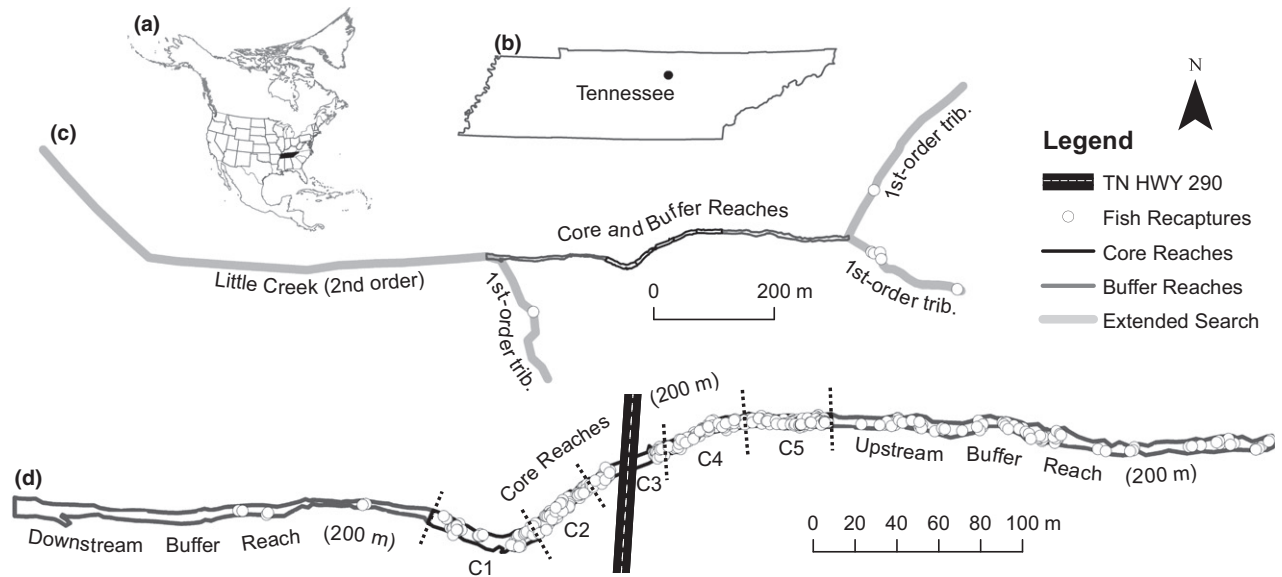


Fig. 1. Study area map illustrating (a) Tennessee in the south-eastern United States, (b) the location of Little Creek in north-central Tennessee (black circle), (c) the portion of Little Creek included in the extended search at the conclusion of the study, and (d) core (C1–C5) and buffer reaches searched during each recapture occasion.

Study area

Tennessee is located in the south-eastern United States, North America (Fig. 1a). Little Creek is a second-order stream located on Tennessee Technological University's Shipley Farm Complex in the Eastern Highland Rim ecoregion in north-central Tennessee (Fig. 1b). Land cover in the catchment is dominated by urbanisation from nearby Cookeville, TN, and a mix of forest, grazed pasture in which cattle have direct stream access, and row-crop agriculture implemented using traditional tillage and spraying practices. The portion of Little Creek used in this study extended from the confluence of two unnamed first-order tributaries at the upstream extent to the mouth of a first-order tributary 600 m downstream (Fig. 1c). Banded sculpin were PIT tagged in five 40 m reaches centred on the State Highway 290 crossing, so that two tagging reaches were downstream (C1 and C2), two tagging reaches were upstream (C4 and C5), and the central tagging reach (C3) was split by the road (Fig. 1d). The culvert underneath State Highway 290 has an open, bedrock bottom and is not a barrier to fish movement. Tagging reaches were buffered upstream and downstream by 200 m search reaches for a total of 600 m.

Materials and methods

Environmental variables

We deployed a HOBO Model U20L Water Level Logger (Onset Computer Corporation, Bourne, MA,

USA) and a metered stage at the downstream extent of the study area to capture temporal variability in hourly water temperature ($^{\circ}\text{C}$) and level. We recorded discharge and stage height every Tuesday following the USGS protocol described by Turnipseed & Sauer (2010), including measuring depth (m) and velocity ($\text{m}\cdot\text{s}^{-1}$) at 20 evenly spaced points across the channel and summing the total volume of water per unit time ($\text{m}^3\cdot\text{s}^{-1}$) across the channel. We used these discharge and stage measurements to construct a rating curve to model continuous stream flow during our study. We also downloaded daily precipitation values obtained from the Upper Cumberland Regional Airport near Sparta, TN (USAF WBAN ID: 723274 99999), for the duration of tracking (NOAA 2015).

Tagging procedure

Banded sculpin were captured on 31 March 2015 within five 40 m core tagging reaches using two backpack electrofishing units (100–125 V direct current) moving in tandem in an upstream direction. Only banded sculpin >70 mm total length (TL) were retained for tagging due to high mortality rates for sculpin smaller than this size (Ruetz et al. 2006) and a sample size of 15 fish per 40 m core reach (total = 75 fish) was targeted to match or exceed sample sizes in similar studies ($N = 41$ – 49 , Breen et al. 2009; $N = 19$ – 92 , Petty & Grossman 2004). The point of capture was recorded for every tagged fish using a Trimble GeoExplorer 6000 Series global positioning satellite (GPS) unit (Trimble Navigation Limited, Sunnyvale, CA, USA). Fish were

anesthetised with tricaine methanesulphonate (MS-222) at 100 ppm buffered with sodium bicarbonate for 2–5 min (Detar & Mattingly 2004) before injection with a 12.45 × 2.02 mm PIT tag (134.2 kHz; TX141ISST; Biomark, Boise, ID, USA) using a 12-gauge syringe. Our tagging procedure followed Ruetz et al. (2006), including using an insertion site into the body cavity just off the midventral line of the body, inserting the needle point into the peritoneal cavity at a 45-degree angle, and then aligned the needle parallel with the body as the tag was deployed. Tag numbers were then recorded using a handheld PIT reader (Model RS601-3; Biomark) and fish were returned to a bucket filled with stream water at the original capture location. Fish were observed for a minimum of 2 h to ensure survival before each individual was scanned again to evaluate PIT tag retention and released at the original capture site.

Recapture procedure

We searched the entire 600 m segment of stream twice per week between April 4 and May 16 (46 days total). On each recapture occasion, scanning was initiated at the downstream boundary and progressed towards the upstream boundary. A multidirectional antenna (Biomark) mounted on a 3-m telescopic pole was used for bank-to-bank scanning keeping the antenna in contact with the water surface in shallow areas (<30 cm depth) and within 30 cm of the benthos in deep areas (>30 cm depth) following the methods of Breen et al. (2009), Black et al. (2010) and Deboer et al. (2015). The antenna was connected to a tuning box and a portable reader (model no. FS2001F-ISO; Biomark) that matched the readers employed to track mottled sculpin by Breen et al. (2009) and Deboer et al. (2015). Upon detection, the ID number from each PIT tag was recorded along with GPS coordinates using the Trimble GeoExplorer 6000. We visually checked for the presence of tagged sculpin and noted when fish flushed because of our tracking activities, but fish were otherwise undisturbed (Breen et al. 2009). We repeated recapture searches every Saturday (4 April through 16 May) and Tuesday (7 April through 12 May) for 46 days to match the temporal extent used to measure short-term dispersal of mottled sculpin in North Carolina (45 days; Petty & Grossman 2004) and Michigan (43–53 days; Breen et al. 2009). At the completion of the study on 16 May, we conducted an extended search (see Fig. 1) for tagged fishes outside of the core and buffer reaches to document maximum displacement and noted any shed tags, which were removed from our analyses.

We conducted two experiments to assess the efficacy of tagging equipment and observers in detecting

tagged fish. First, we injected 10 PIT tags oriented longitudinally in fish-shaped agarose gels to simulate being implanted within a fish and then hid the gels in a 50 m reach of Little Creek. Without knowledge of tag locations, five independent observers scanned the 50 m reach using the sweeping protocol described above and the number of tags successfully detected was recorded to estimate detection probability. Second, without knowledge of the observers operating the scanner, a decoy tag was placed in a WHIRLPAK (Nasco, Fort Atkinson, WI, USA) weighted down by a rock and hidden in the stream during all recapture occasions. The proportion of times this decoy tag was successfully detected was used as a secondary measure of detection efficiency.

Movement analyses

We analysed movement for banded sculpin recaptured at least three times during our tracking study. Coordinates for each sculpin position were differentially corrected as described in detail by Breen et al. (2009) to ensure submetre accuracy for recorded locations. We used program GPS Pathfinder Office (Trimble Navigation Limited) to import coordinates from the handheld Trimble unit, computed differential corrections using base station data archived by the Tennessee Department of Transportation District 24 station (8 km from study site) and then exported corrected coordinates to ArcMap 10.2 (Environmental System Research Institute, Inc., Redlands, CA, USA). We then used ArcMap 10.2 to calculate the longitudinal distance (m) between recapture events and the original tagging position for each fish on each recapture occasion using the centreline of the stream to estimate dispersal distance (Breen et al. 2009). From these data, we constructed frequency histograms (bin width = 10 m) of signed movement distances in which upstream movement was given a positive sign and downstream movement was given a negative sign (Petty & Grossman 2004). We tested normality and kurtosis of each distribution using D'Agostino's test for normality and Anscombe-Glynn's test of kurtosis (Petty & Grossman 2004; Hudy & Shiflet 2009). We tested for directionality bias by comparing upstream and downstream movement distances using chi-square tests (Skalski & Gilliam 2000; Hudy & Shiflet 2009).

Our first objective was to test the efficacy of predictive dispersal models based on fish morphology, stream size and time. Radinger & Wolter (2014) used multiple regression to develop parameters for fitting leptokurtic dispersal kernels based on fish total length (mm), caudal fin aspect ratio (Sambalay 1990), stream order (Strahler 1957) and time (days) between observations. This modelling framework was recently

developed in the *fishmove* package for program R (Radinger et al. 2014). We used the *fishmove* package to construct leptokurtic dispersal models specific to each recapture occasion to assess temporal variability in dispersal predictions using the equation:

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

where p is equal to the share of the stationary component of the total population, σ_{stat} is equal to the mean movement distance of the stationary component of the population, and σ_{mob} is equal to the mean movement distance of the mobile component of the population. We parameterised the underlying multiple regression models used to fit leptokurtic dispersal kernels in *fishmove* with the median value for all species in the genus *Cottus* as reviewed by Radinger & Wolter (2014), including total length equal to 74 mm, caudal fin aspect ratio equal to 1.18, stream order equal to 2 and time interval equal to each of our recapture occasions (days = 4, 7, 11, 14, 18, 21, 25, 28, 32, 35, 39, 42 and 46). Dispersal models for each recapture occasion were weighted by total number of fish observed during that tracking session to generate the expected number of fish at each distance away from the tagging location. Expected frequency distributions were compared to observed frequency distributions calculated from data collected during each recapture occasion using the site of tagging as the origin of dispersal. We used Kolmogorov–Smirnov (KS) tests to assess model fit by comparing the observed number of fish during each recapture occasion to the number of fish expected according to leptokurtic dispersal kernels (Petty & Grossman 2004).

Our second objective was to assess variability of stationary and mobile components of the banded sculpin population in Little Creek. We used the *fishmove.estimate* function from the *fishmove* package in program R to generate estimates (and 95% confidence intervals) of proportion of stationary fishes (p), average distance moved by stationary fish (σ_{stat}) and average distance moved by mobile fish (σ_{mob}) based on data obtained from our 13 recapture occasions. We first compared temporal variation in these parameters estimated using our field data to the median and 95% confidence intervals for p (median = 0.68, CI = 0.07), σ_{stat} (3.86, 3.24) and σ_{mob} (55.59, 24.72) for all *Cottus* species reviewed in Radinger & Wolter (2014). We considered differences significant if confidence intervals did not overlap. Next, we tested for a relationship between flow pulses and water temperature (predictor variables) and fish movement (σ_{mob} ;

response variable). As movement by the mobile component is modelled as constant diffusive spread through time (Skalski & Gilliam 2000; Rodríguez 2002), we used residual values estimated from the linear relationship between time and σ_{mob} to estimate higher than average movement (positive residual values), lower than average movement (negative residual values) and average movement (residual value = 0) for each recapture occasion. We then tested for the effect of flow pulses and temperature increases on movement by regressing residual values (response variable) against maximum flow pulse ($\text{m}^3 \cdot \text{s}^{-1}$) and maximum water temperature ($^{\circ}\text{C}$) for each recapture occasion. Finally, to facilitate comparison with previous *Cottus* movement studies, we tested for a linear relationship between fish size (TL, mm) and maximum as well as median displacement distances (m) to evaluate size-specific movement following the methods of Breen et al. (2009).

Our third objective was to determine occurrence and extent of switching between stationary and mobile dispersal behaviours by individual fish. We constructed a frequency histogram of the number of times individual recaptured fish switched between being classified as stationary (S, recapture distance $\leq \sigma_{\text{stat}}$ from tagging location for a recapture occasion) and mobile (M, recapture distance $> \sigma_{\text{stat}}$ distance from tagging location) between subsequent recaptures while ignoring nondetections. For example, a fish with dispersal history ‘SSS0MSSSSSSSS’ across the 13 recapture occasions switched between stationary and mobile two times with nondetection during recapture occasion four. Estimates from *fishmove.estimate* were used to assign individual fish to stationary or mobile components for each recapture occasion. We repeated this process for all individuals retained for movement analysis to construct a frequency distribution of the number of switches observed during tracking. We analysed this distribution using D’Agostino’s test for normality (Petty & Grossman 2004) and Anscombe–Glynn’s test of kurtosis (Hudy & Shiflet 2009). All statistical analyses were conducted in program R version 3.1.2 (R Development Core Team 2015).

Results

We tagged 79 banded sculpin throughout the core reaches on 31 March 2015. Tagged fish ranged 71–137 mm total length and weighed 4.8–32.5 g. Seventy-one fish were recaptured at least once, 51 of which were recaptured ≥ 3 times and were retained for movement analysis. Six shed tags were recovered from the stream and were excluded from analysis. Detection of tags during two detection probability experiments was high, including on average 94%

Table 1. Estimates of normality (skewness), kurtosis and upstream versus downstream bias in movement by banded sculpin tracked in Little Creek, TN, during 4 April through 16 May 2015.

Day	<i>N</i>	Detection	SE	Skewness	<i>P</i> -value	Kurtosis	<i>P</i> -value	# US	# DS	Chi-Square	DF	<i>P</i> -value
4	34	0.67	0.07	4.41	<0.001	21.49	<0.001	20	1	108.95	4	<0.001
7	37	0.73	0.06	4.60	<0.001	23.70	<0.001	17	6	126.79	7	<0.001
11	30	0.59	0.07	4.59	<0.001	22.64	<0.001	15	3	200.00	7	<0.001
14	32	0.63	0.07	4.98	<0.001	27.41	<0.001	13	3	201.00	5	<0.001
18	43	0.84	0.05	4.24	<0.001	20.41	<0.001	27	5	136.87	17	<0.001
21	28	0.55	0.07	4.33	<0.001	22.47	<0.001	16	3	127.35	11	<0.001
25	32	0.63	0.07	4.09	<0.001	21.17	<0.001	18	4	203.00	11	<0.001
28	31	0.61	0.07	4.33	<0.001	23.09	<0.001	21	4	184.81	11	<0.001
32	28	0.55	0.07	3.89	<0.001	20.32	<0.001	19	5	180.22	11	<0.001
35	25	0.49	0.07	3.92	<0.001	18.47	<0.001	16	3	177.69	10	<0.001
39	20	0.39	0.07	3.57	<0.001	15.83	<0.001	12	3	172.24	8	<0.001
42	18	0.35	0.07	3.03	<0.001	12.01	<0.001	11	3	167.26	7	<0.001
46	12	0.24	0.06	2.25	<0.001	6.90	<0.001	8	2	198.00	11	<0.001

The number of fish recaptured (*N*), proportion of tagged fish detected and the number of fish moving at least 1 m upstream (# US) and 1 m downstream (# DS) are given.

(range 80–100%) for the experiment with hidden tags and 100% detection of the decoy tag during recapture occasions. Despite high detection capability, the proportion of the 51 tagged fish detected during each recapture ranged 0.24–0.73 and generally declined with time (Table 1).

Distances moved were not normally distributed and fit a leptokurtic pattern. Movement frequency distributions were positively skewed (tail towards upstream) during all recapture occasions (skewness >2.0, *P* < 0.01 for all dates) but generally became less skewed with time (Table 1). All frequency distributions were characterised by significant leptokurtosis (kurtosis >6.9, *P* < 0.01 for all dates) and a greater number of fish dispersed upstream compared to downstream ($\chi^2 > 108$, *P* < 0.01 for all dates). Leptokurtic dispersal kernels correctly characterised frequency histograms of signed dispersal distances for all but one recapture occasion (Fig. 2). The predicted leptokurtic dispersal kernel for Day 18 differed (*D* = 0.52, *P* < 0.01) from the observed fish distributions when 27 of the 43 recaptured fish moved upstream, eight of which moved greater distances than expected. Fish size (TL) predicted neither median ($F_{1,50} = 0.58$, *P* = 0.45, *R*² = 0.01) nor maximum ($F_{1,50} = 0.13$, *P* = 0.71, *R*² < 0.01) displacement distances.

Banded sculpin movement was temporally dynamic. The proportion of stationary fish (*p*) was not static through time and differed (i.e. nonoverlapping confidence intervals) from expected for five of the 13 recapture occasions (Fig. 3a). Departures from the static, expected value of *p* increased with time so that *p* was consistently less than expected during the latter portion of the study. The decrease in *p* was associated with an increase in σ_{mob} calculated without regard to upstream or downstream directionality

(Fig. 3b) and estimates of σ_{mob} differed from expected for seven of the 13 recapture occasions. Estimates of σ_{stat} did not differ from expected for any of the recapture occasions (Fig. 3c).

Precipitation events caused elevated stream flows and punctuated high pulse events on three occasions, including 5 April, 11 April and 17 April (Fig. 4a). Precipitation events generally caused short-term (<3 days) declines in water temperature until a dry period with no precipitation and subsequent declining flows caused increased water temperatures between 2 May and 16 May. Linear regression fitted to the relationship between time and σ_{mob} illustrated variability in movement among recapture occasions expressed as positive, negative and near-zero residual values (Fig. 4b). Residual values were not related to maximum temperature values ($F_{1,11} = 0.93$, *P* = 0.36, *R*² = 0.08) but were positively correlated with maximum flow pulse magnitude ($F_{1,11} = 7.49$, *P* = 0.02, *R*² = 0.40) measured during each recapture occasion so that the largest residual value for movement corresponded with the largest recorded flow pulse (Fig. 4c). The relationship between movement residuals and flow pulse magnitude was driven by the single large pulse so that the test was not significant ($F_{1,10} = 0.6$, *P* = 0.45, *R*² = 0.06) when the recapture occasion with the large pulse (occasion 5) was removed.

Banded sculpin dispersal included switching between stationary and mobile movements by some individuals. Twenty-three (45%) fish were classified as only stationary or mobile during every recapture event during which they were detected. Twenty-eight (55%) fish switched between stationary and mobile movement behaviours at least once. Among the fish that switched, nine fish switched once, 10 switched twice, three fish switched three times, one fish

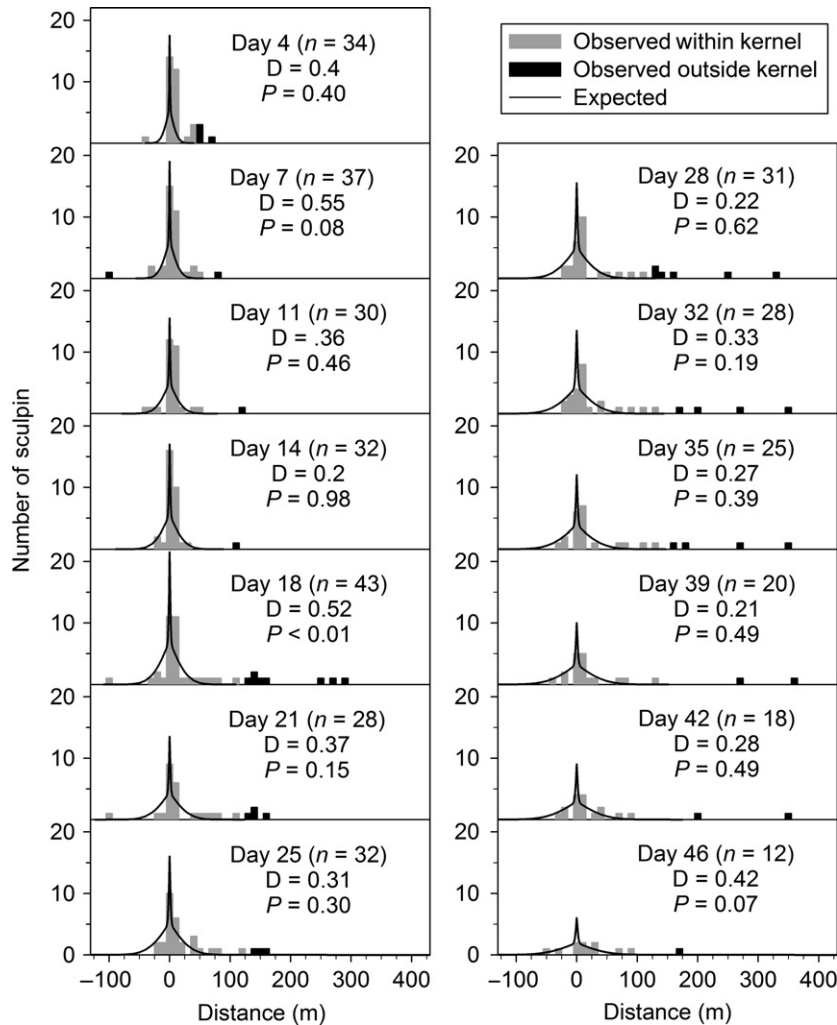


Fig. 2. Frequency distributions for expected movement distances based on leptokurtic dispersal models (black line) and observed movement distances within (grey bars) and outside (black bars) the expected range for banded sculpin in Little Creek, TN, on 13 recapture occasions during April and May 2015. Positive and negative values along the x-axis represent upstream and downstream movements respectively. Results of Kolmogorov–Smirnov tests for differences between observed versus expected frequency histograms are given (see text for details).

switched four times, four fish switched five times, and one fish switched seven times (Fig. 5). The distribution of switching behaviour was skewed (skewness = 1.40, $Z = 3.68$, $P < 0.01$) and was leptokurtic (kurtosis = 4.39, $Z = 1.98$, $P = 0.02$).

Discussion

Our study empirically showed short-term movement of banded sculpin was leptokurtic, temporally dynamic, and included stationary and mobile components between which some individuals switched. Each of these processes operated at spatial scales broader than expected based on historical accounts of the species residing within 6 m of stream (Greenberg & Holtzman 1987). We also found that a large flow pulse stimulated increased dispersal so that a leptokurtic dispersal kernel did not accurately predict fish movement immediately (within 2 days) following the pulse, but movement again matched a leptokurtic pattern by the next recapture occasion. Movement was also heterogeneous at the scale of

individuals. The majority of fish switched between mobile and stationary movement behaviours and the overall pattern of switching was leptokurtic and characterised by many fish switching few times and few fish switching many times. Despite heterogeneity in movement at the population and individual scales, diffusive spread of banded sculpin occurred during our study (Skalski & Gilliam 2000) as predicted by leptokurtic dispersal models (Radinger & Wolter 2014).

Movement by banded sculpin during our study matched patterns documented for multiple *Cottus* species, including upstream-biased movements operating on broader-than-expected scales. Although our study was conducted over a relatively short temporal extent, we detected movement distances greater than those reported for most *Cottus* fishes reviewed by Hudy & Shiflet (2009). Similarly, our findings reflect recent documentation of minimally restricted movement by mottled sculpin (Breen et al. 2009) and upstream-biased movement of Potomac sculpin *Cottus girardi* (Hudy & Shiflet 2009). In our study,

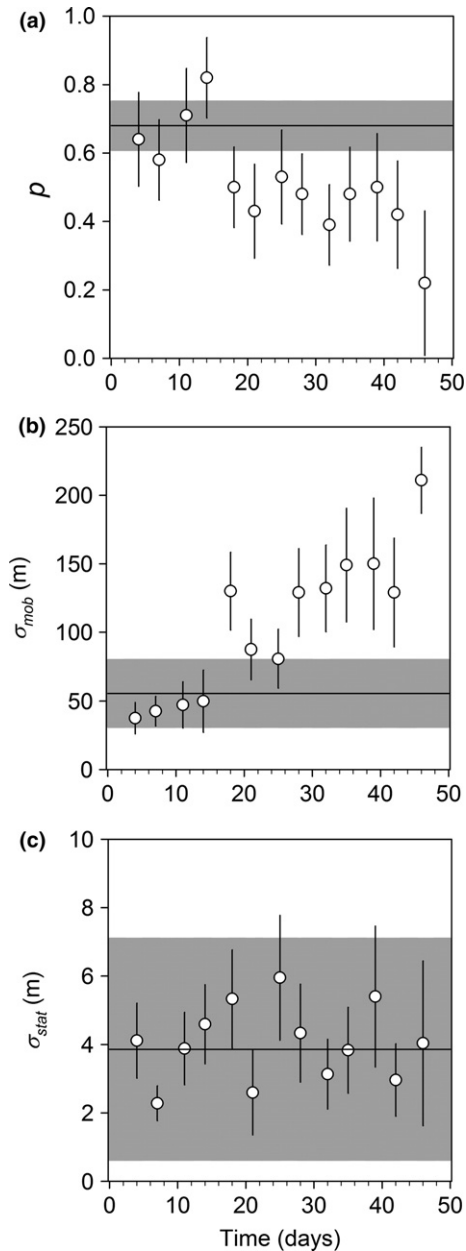


Fig. 3. Estimates of means ($\pm 95\%$ confidence interval) for (a) the shared proportion of stationary (p), (b) the mean movement distance of mobile (σ_{mob}) and (c) mean movement distance of stationary (σ_{stat}) banded sculpin for 13 recapture occasions. Solid lines and shaded areas represent median and 95% confidence intervals, respectively, reported for all *Cottus* species by Radinger & Wolter (2014).

departures from expected values of p and σ_{mob} were at least partially due to the limited temporal and spatial extent of our investigation. Our study closely matched the time periods employed by Petty & Grossman (2004) and Breen et al. (2009) to measure within-season movement of congeneric fishes, but we did not measure movement at an annual timescale. This is, in part, because the number of fishes detected within the study area was greatly reduced by the end

of our study and our study reach was too small given what we now know about banded sculpin movement. During design of our study, we assessed what was known for banded sculpin and found they were known to use only 6 m of stream (Greenberg & Holtzman 1987). Although we designed our study to capture the maximum expected movement of such a restricted species (Albanese et al. 2003), dispersal was greater than expected most likely because the previously reported value (i.e. 6 m; Greenberg & Holtzman 1987) only captured the stationary component (i.e. up to 6 m in this study). In fact, we know our estimates of p and σ_{mob} were conservative based on documentation of fish exiting the buffer reaches during the extended search conducted as a part of our final recapture occasion. Additionally, there was an incidental recapture (and release) of an individual 518 m downstream on 17 April during unrelated research in Little Creek (A. Gebhard, *unpublished data*). Thus, our findings support conclusions by Gowan et al. (1994) and Rodríguez (2002) in that even well-planned movement studies can underestimate movement by highly mobile fishes, which can ultimately inhibit conservation of stream fishes (Cooke et al. 2012).

We found some evidence that banded sculpin movement was related to stream flow variability. The largest shifts in p and σ_{mob} corresponded exactly with the recapture occasion that followed the largest flow pulse observed during our study. After the pulse, the mean proportion of stationary fish declined from >0.8 to <0.5 and σ_{mob} increased from 50 m to 125 m over the course of 2 days, and to our knowledge, no other major change to the stream occurred during this period. Although this pattern is suggestive, our correlative observation is based on a single large pulse. Previous studies have challenged the notion that flow pulses affect sculpin movement or density (Anderson 1985; Hudy & Shiflet 2009) and additional research is needed to document fish responses to flow pulses. In terms of low flow, our study captured the transition from flows regularly sustained by precipitation to a period of zero rainfall and low discharge. Across this strong hydrologic gradient, diffusive spread of banded sculpin continued uninterrupted. This observation is consistent with conclusions by Grossman et al. (2010), who hypothesised that fish disperse upstream during low flow periods when the ‘hydrodynamic barrier’ is weakest. Our study area is free of perched road culverts that act as small waterfalls to block fish dispersal (Perkin & Gido 2012), so banded sculpin upstream dispersal was possible even during periods of reduced stream flow. Smaller, headwater streams such as the unnamed first-order tributaries at the upstream extent of our study area are sensitive to local extirpations

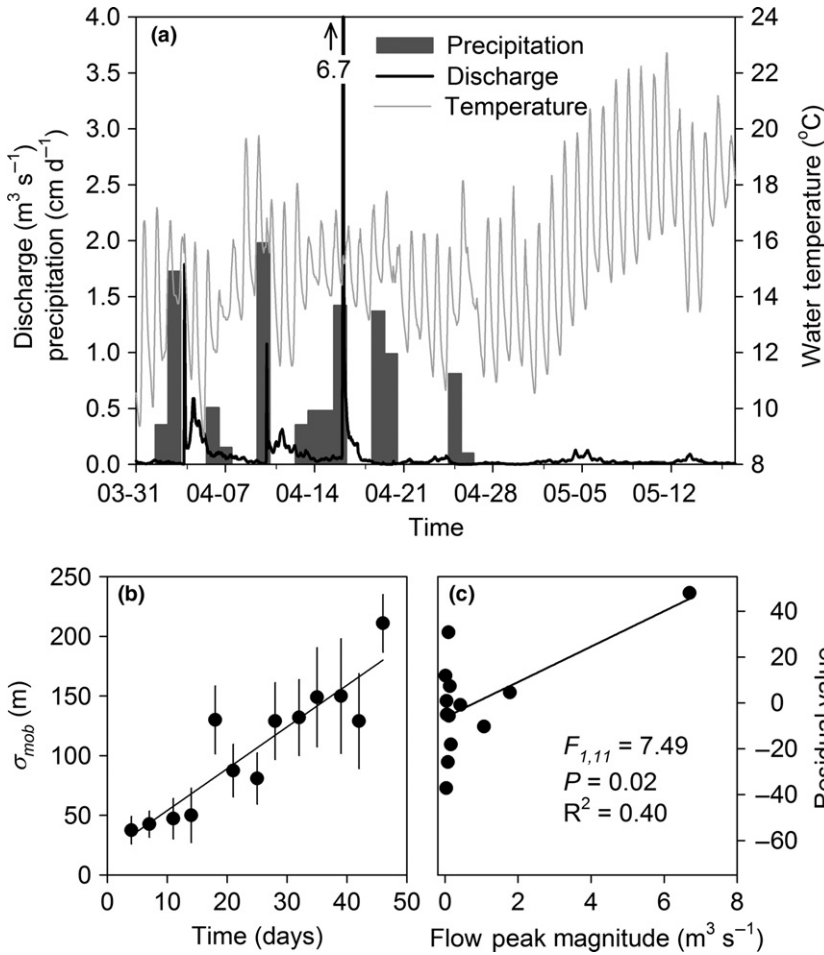


Fig. 4. (a) Temporal change in daily precipitation (dark grey bars), hourly stream discharge (black line) and hourly stream temperature (grey line) for Little Creek, TN, during April and May of 2015. Major ticks on x-axis represent recapture occasions. (b) Relationship between time and distance moved by the mobile component (σ_{mob}) with a fitted regression line from which residuals were measured, and (c) relationship between residual values and peak stream flow values for each recapture occasion.

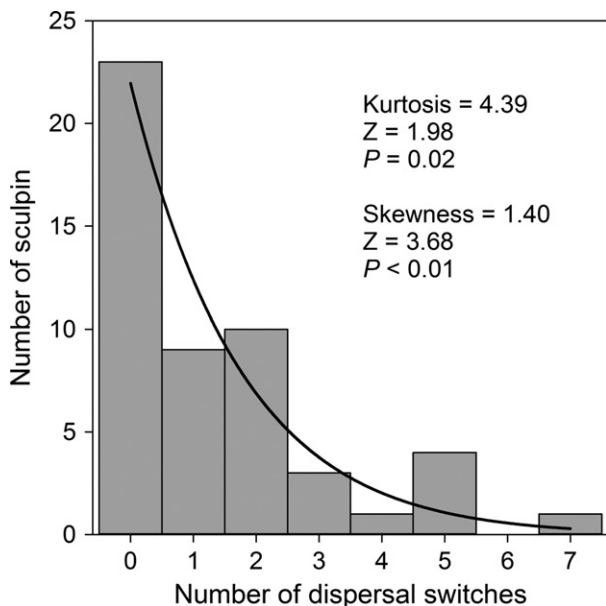


Fig. 5. Frequency of switching between mobile and stationary movement behaviours for banded sculpin tracked on 13 recapture occasions during April and May 2015 in Little Creek, TN. The frequency of switching was positively skewed and leptokurtic.

caused by natural disturbances and thus require continued colonisation from downstream source populations (Schlosser 1987). We hypothesise that consistent, upstream marching by banded sculpin as well as other *Cottus* species (Breen et al. 2009; Hudy & Shiflet 2009) is a mechanism for sustaining head-water populations through the meta-population framework (Levins 1969).

Banded sculpin movement behaviour varied at the scale of individuals, including switching between stationary and mobile dispersals by more than 50% of individuals. We found 23 fish did not switch, and the remaining 28 were partitioned among one, two, three, four, five and seven switches. This pattern resulted in a skewed, leptokurtic distribution of switches by banded sculpin. Sculpin switching behaviour was suggested for mottled sculpin by Petty & Grossman (2004) and observed for bullhead *Cottus gobio* by Knaepkens et al. (2005). Nonuniform switching behaviour implies there are intrinsic and/or extrinsic mechanisms involved with dispersal decisions. One potential extrinsic mechanism involves changes in habitat volume with flow variability and associated changes in density-dependent interactions among

banded sculpin (Downhower et al. 1990; Koczaja et al. 2005). Intrinsic mechanisms affecting movement behaviour are less obvious. Spawning of banded sculpin is largely unstudied but presumed to occur from January to February (Williams & Robins 1970) and possibly into early April (Smith 1979). If spawning in Little Creek continued into April, then our study captured the end of the spawning season when males might have been switching from stationary behaviours while guarding young to mobile behaviours as nests were abandoned (e.g. Knaepkens et al. 2005). We attempted to assign sex to fish recaptured at the completion of our study, but only six fish were successfully captured and gonads were not well developed, thus precluding rigorous statistical analysis. These questions could be answered by further research connecting switching to individual sexes during a known spawning period. On-going work in Little Creek (A. Gebhard, *unpublished data*) will define sexual dimorphism (useful for assigning sex to tracked fish) and reproductive life-history traits (useful for defining spawning season) that will allow future testing of reproduction-based movement hypotheses. Regardless, our findings advance evolution of the RMP (Gowan et al. 1994) by revealing that not only do populations consist of mobile and sedentary components (Skalski & Gilliam 2000; Rodríguez 2002), but that fishes apparently switch between these behaviours multiple times during their lifetime.

Our study provided a brief trajectory of movement characteristics for banded sculpin. Despite the short-term extent of our investigation, banded sculpin moved further than expected (Greenberg & Holtzman 1987), movement followed an increasingly unifying theme in fish movement (i.e. leptokurtosis, Radinger & Wolter 2014), the population responded to a large flow pulse that stimulated movement and individuals frequently switched between stationary and mobile behaviour. If viewed individually, none of these properties would have revealed the emergent property discovered by a collective view: constant upstream movement expressed as diffusive spread across space and through time (Skalski & Gilliam 2000). This emergent property represents an apparent paradox, in which upstream movement continues despite individual- and population-scale temporal heterogeneity in movement. We suggest this paradox represents the march of the sculpin, in which constant arrival of individuals at headwater streams mediates density-dependent ecosystem effects (Flecker 1984) and links local community properties with regional processes (Taylor 1996). Such landscape-scale perspectives in fish ecology (Schlosser 1991) enhance our understanding and predictability of fish movement and ultimately aid in freshwater resource conservation and management (Cooke et al. 2012; Day et al. 2016).

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