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Mike Booth
Cornell University

Nelson Hairston
Cornell University

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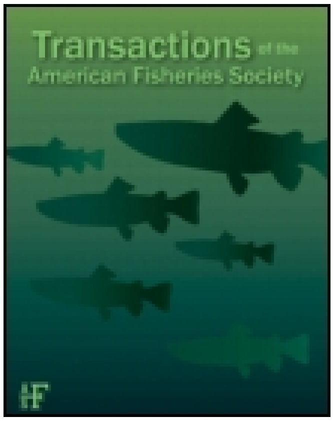

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Michael T. Booth[a][b], Alexander S. Flecker[a] & Nelson G. Hairston Jr.[a]
[a] Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14850, USA
[b] Present address: United Water Conservation District, 106 North 8th Street, Santa Paula, California 93060, USA.
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ARTICLE

Is Mobility a Fixed Trait? Summer Movement Patterns of Catostomids using PIT Telemetry

Michael T. Booth,*[1] Alexander S. Flecker, and Nelson G. Hairston Jr.
Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14850, USA

Abstract

Fish populations are composed of a mixture of sedentary and mobile individuals, but it is not clear whether movement behavior is plastic or fixed for individuals and what proportion of the population exhibits mobile behavior. To investigate the mobility and movement patterns of two common species of suckers, the Sonora Sucker *Catostomus insignis* and the Desert Sucker *Catostomus clarkii*, in the Gila River of western New Mexico, we tracked 449 individuals over three summers using passive integrated transponder (PIT) telemetry. Both species were mobile and the typical linear home ranges for mobile individuals exceeded 150 m, but approximately 25% of individuals were detected only in a single habitat segment. We observed increased movement after spates caused by summer monsoon rains, and fish used areas of the stream differently under high- and low-flow conditions. Fish moved farther between years than within years, but a subset of individuals were found in the same locations from year to year. For the study species, movement behavior does not appear to be a fixed trait for individuals, and many individuals exhibited both stationary and mobile behavior among years. We also investigated whether sample size biased the estimates of movement parameters. We concluded that movement parameters would be underestimated by 20–50% if we had tracked fewer individuals, but the degree to which the parameters were biased varied from year to year.

Movement of organisms at some scale is ubiquitous in all ecosystems and regulates not only the fate of individuals but the structure and dynamics of ecosystems, communities, and populations (Nathan et al. 2008). For example, large-scale movements of fish can influence subsidies among ecosystems (Flecker et al. 2010) as well as recolonization following habitat alteration (Gowan and Fausch 1996). Understanding movement dynamics is especially important for managing fisheries because movement regulates the connectivity among populations, dispersal to and colonization of new habitats, and interactions among species. Large-scale movements are often necessary for reproduction, avoiding adverse habitat or resource conditions, or dispersal (Bryant et al. 2009; Flecker et al. 2010; Young 2011).

Movement behavior may vary within and among species (Fraser et al. 2001; Rodríguez 2002) as well as within the same species among different environments (Woolnough et al. 2009) and life history stages (Young 2011), making generalization of movement patterns difficult. Advances in tracking technology like passive integrated transponder (PIT) telemetry (Roussel et al. 2000; Zydlewski et al. 2006; Teixeira and Cortes 2007) have revealed that in many fish populations at least a portion of the individuals are mobile. This mobile–sedentary distinction is statistically consistent with the leptokurtic movement distributions observed in many stream fishes (Skalski and Gilliam 2003). However, conclusions about the movement distributions of fishes are generally based on data collected within a single season (reviewed in Rodríguez 2002) or small numbers of individuals, which may be problematic for estimates of many movement parameters (Börger et al. 2006). There is evidence that both individuals and populations show substantial variation in movement patterns over time (Young 2011); tracking large numbers of individuals within a population can elucidate whether the proportion of mobile individuals changes depending on environmental conditions and whether movement behavior is fixed or plastic for individuals (Rodríguez 2002).

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*Corresponding author: mike.booth@cornell.edu

[1] Present address: United Water Conservation District, 106 North 8th Street, Santa Paula, California 93060, USA.

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A fundamental assumption of movement studies is that the behaviors of individuals selected for tracking are representative of the organisms and populations of interest and that the monitoring method adequately captures these movement patterns without altering fish behavior. Movement studies are often limited by the numbers of fish tracked (e.g., radiotelemetry) or the spatial and temporal resolution of the data collected (mark–recapture). Low-cost passive integrated transponder (PIT) tag telemetry makes it possible to track large numbers of animals over fairly broad spatial scales, although this technology is only effective in small- to moderate-sized wadeable streams due to its relatively small detection distances (up to about 1 m; Cucherousset et al. 2005; Linnansaari et al. 2007). While radiotelemetry has advantages over PIT telemetry in terms of spatial scale and temporal resolution for individual fish (Lucas and Baras 2000), results based on limited numbers of animals may not be robust or representative of the movement patterns of the population as a whole (Börger et al. 2006).

In many streams (Lee et al. 1980), and particularly in much of the American Southwest (Minckley 1973; Sublette et al. 1990), nongame species (e.g, catostomids and cyprinids) compose a substantial fraction, if not the dominant portion, of the fish community. There is limited knowledge of movement patterns for many common fish species in the Southwest, and most studies have been limited to endangered taxa like the Razorback Sucker *Xyrauchen texanus* in large rivers (Tyus and Karp 1990; Modde and Irving 1998; Mueller et al. 2000). Large rivers in the Southwest have experienced extensive human modification of temperature regime, flow, and sediment load, often at great cost to the native species (Rinne and Miller 2006). Movement provides important linkages among populations and habitats; understanding how native species move within this landscape is critical to managing and conserving these fisheries.

We focus here on the locally abundant Sonora Sucker *Catostomus insignis* and the Desert Sucker *Catostomus clarkii,* which can provide insight into the variation in movement patterns within and among species. Previous work in small streams found greater mobility in Desert Suckers than Sonora Suckers as well as variation in movement behavior among streams (Booth and Shipley 2012), while no movements were detected among the few fish recaptured in a larger stream, the Gila River (Bestgen et al. 1987). Concurrent with the present study, we investigated small-scale, short-term movement behaviors and found high but variable rates of population turnover at the habitat scale, distinct diel patterns in movement behavior, and high site fidelity despite extended forays elsewhere for both suckers in the Gila River (Booth et al. 2013). Our focus in this complementary study was to address movements on a larger spatial scale (hundreds of meters to kilometers) over multiple years and to assess the degree to which sample size influences the estimates of movement parameters. We collected movement data on 449 PIT-tagged fish over a 3-year period and detected most animals (>70%) multiple times. Our primary goal in this study was to describe the movement patterns within and between the two species as well as among years. We also investigated whether movement behaviors are fixed for individuals and used sequentially larger portions of this data to assess how the number of individuals studied influences movement parameters.

STUDY LOCATION

The upper Gila River is a tributary to the Colorado River that originates in the Mogollon Mountains of western New Mexico and that is one of the few remaining free-flowing rivers in the western United States. Our study site was located at the Heartbar Wildlife Area, New Mexico, near the confluence of the West and Middle Forks of the Gila River, approximately 3 km downstream from Gila Cliff Dwellings National Monument. Flow in the Gila River is driven by snowmelt, and the region also experiences a summer monsoon season (July–September), which can account for a substantial proportion of the total annual rainfall (Sheppard et al. 2002). The wetted width of the river during summer ranged from 7 to 14 m but was variable within seasons due to spring runoff, summer dry periods, and monsoonal thunderstorms. The mean ± SD water temperature for the period from May to July was 19 ± 3°C (range, 11–32°C) in 2008, 21 ± 4°C (11–33°C) in 2009, and 19 ± 3°C (13–26°C) in 2010. The estimated median river discharge during the same period was 0.63 m^3/s (range, 0.24–4.54 m^3/s) in 2008, 0.23 m^3/s (0.11–8.84 m^3/s) in 2009, and 0.62 m^3/s (0.20–3.05 m^3/s) in 2010. The study reach has a predominantly riffle–pool structure with wide shallow runs and occasional beaver dams. There is a limited riparian forest of Fremont cottonwood *Populus fremontii* and Arizona sycamore *Platanus wrightii* and smaller shrubs. Pool habitats are formed by large woody debris, undercut banks, canyon walls, and large boulders and contain depositional sediments (silt, sand, and gravel substrata).

Although Sonora Suckers and Desert Suckers had similar abundances as juveniles, adult Sonora Suckers were typically more abundant than adult Desert Suckers in the West Fork Gila River (M. Booth, unpublished data; juvenile ratio, 0.9:1; adult ratio, 5.8:1). Native Gila Trout *Oncorhynchus gilae,* Headwater Chub *Gila nigra,* Longfin Dace *Agosia chrysogaster*, Speckled Dace *Rhinichthys osculus*, and Spikedace *Meda fulgida* were also present, along with introduced species from the Ictaluridae, Salmonidae, Centrarchidae, Cyprinindae, and Poeciliidae families (though these were substantially less abundant than the suckers, i.e., <10% of the total fish biomass).

METHODS

Study Species

The Sonora Sucker and Desert Sucker occur in a broad range of stream habitats, ranging from high-elevation headwaters to lowland warmwater desert streams in Arizona and New Mexico (Minckley 1973). The Sonora Sucker typically feeds on invertebrates and detritus (Schreiber and Minckley 1981; Pilger et al. 2010) and is abundant in deeper pools with restricted flow and fine substrates (Minckley 1973), where it is often found in large aggregations (>30 individuals; Booth et al. 2013). The Desert Sucker has cartilaginous edges on its jaws, allowing it to scrape algae off the substrate (Minckley 1973; Minckley and Marsh 2009). For adults of both species, limited foraging occurs during the day, with most activity occurring during low-light periods (Booth et al. 2013). In the West Fork Gila River, adults of both species typically take refuge in deep pools (>1 m) or beneath overhead structure during the day and move into shallow-water areas (<0.3 m) at night to feed (Booth et al. 2013).

Movements

Mapping.—Each season, we mapped the study reach using a GPS (Vista Cx; Garmin International, Olathe, Kansas); characterized the habitat type, substrate, width, depth, flow, and presence of "refuge" features (e.g., woody debris, undercut banks); and created a GIS map using Manifold GIS 8.0 (Manifold Software Limited, Hong Kong). Because fish stayed in refuges during the day (when our surveys were performed) fish locations could be described as discrete habitat units (typically pools or debris piles), and we calculated all distance measures between the centers of these habitat units.

Tagging.—The tagging reach studied was 1.8 km long; it was flanked by an extended reach (1.3 km downstream and 1.0 km upstream) that was used to detect movements outside of the tagging reach. In the central tagging reach, fish were captured for tagging using electrofishing and hoop or fyke nets. An electrofishing survey of the entire reach was completed in early June each year as part of larger monitoring efforts at the site. Additional collection efforts were distributed throughout the remainder of the 2008 and 2009 seasons and focused on pool habitats suitable for hoop and fyke nets (Figure 1). Each

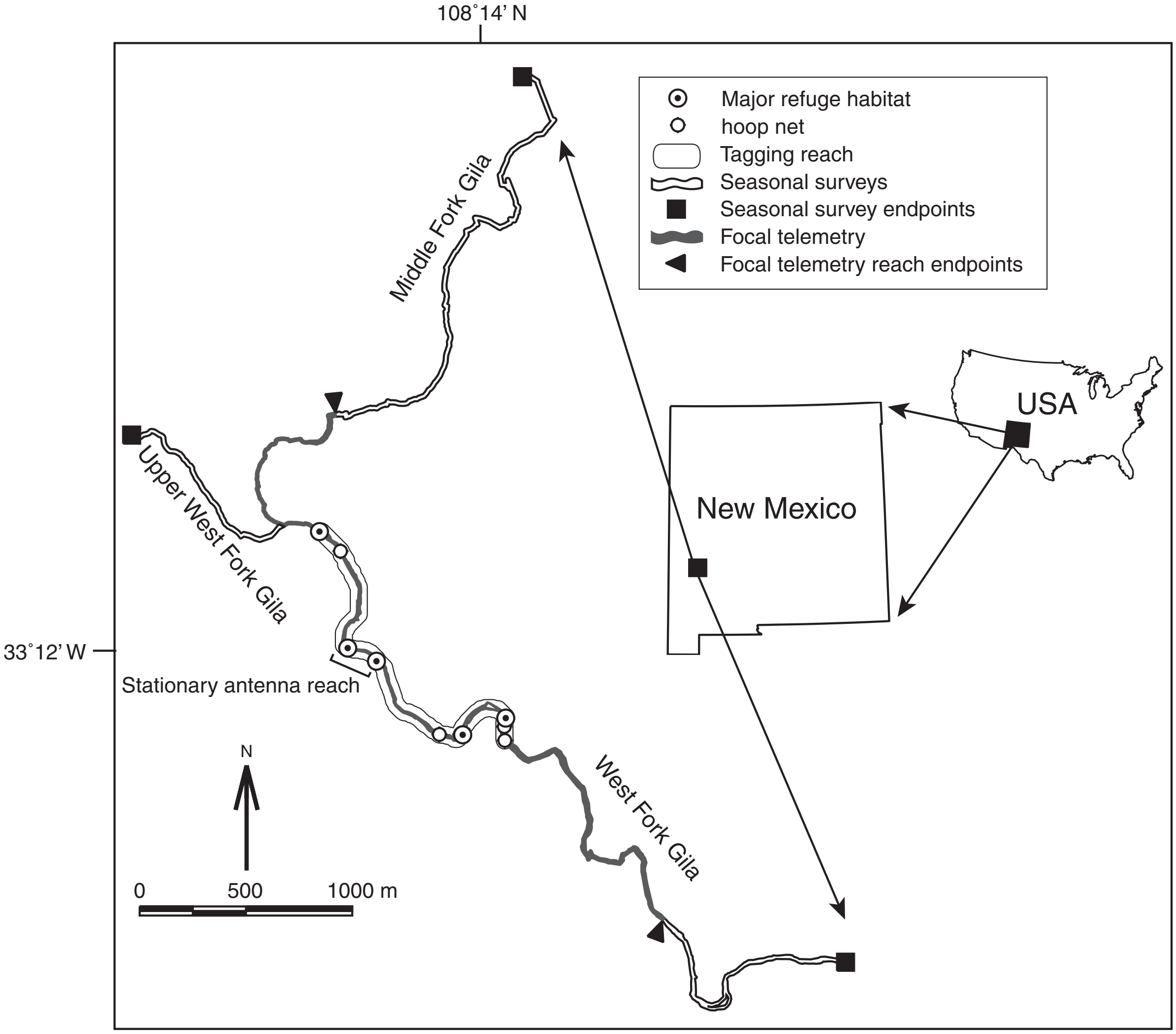

FIGURE 1. Map of the upper Gila River. The tagging reach was downstream of the confluence of the upper West Fork and Middle Fork Gila rivers. The gray-shaded section of stream bracketed by black triangles is the full reach regularly surveyed using portable PIT telemetry. Unshaded areas of stream indicate reaches that were sampled for tagged fish once each year via PIT telemetry or electroshocking. The locations where fish were captured via hoop nets and major refuge habitats (also sampled using hoop nets) within the tagging reach are indicated by circles. Eight stationary PIT antennas were installed in the central portion of the tagging reach during 2009 and 2010.

TABLE 1. Standard lengths of fish tagged with passive integrated transponder tags each year in the upper Gila River.

			Standard length (mm)	
Species	Tagging year	N	Mean ± SD	Range
Sonora Sucker	2008	233	268 ± 79	100–415
	2009	174	259 ± 76	145–464
	2010	24	211 ± 49	152–310
	Total	431	261 ± 77	100–464
Desert Sucker	2008	73	186 ± 43	104–370
	2009	37	194 ± 37	150–292
	2010	9	210 ± 41	153–294
	Total	119	190 ± 41	104–370

fish captured was weighed (electronic balance or spring scale), measured (length [mm]), tagged, and had its capture location recorded. If a previously tagged fish was recaptured, we weighed and measured it to estimate growth. We tagged all adult and subadult Sonora Suckers and Desert Suckers captured from 2008 to 2010 (May–July; Table 1). Read–write half duplex PIT tags (RI-TRP-WEHP: 134.2 kHz, 23 × 3.85 mm, 0.6 g in air; Texas Instruments, Dallas, Texas) were implanted in the body cavity of the fish using a scalpel to make a small incision just below the pectoral fin and a tag injector to inject the tag (MK-10 implanter; BioMark, Boise, Idaho). Tag weight was typically much less than 1% of fish body mass. Injectors and scalpels were sterilized in 95% ethyl alcohol. The incision was coated with an antiseptic liquid bandage (New Skin). Each fish was released in the same location in which it was captured or recaptured and observed until activity returned to normal. We held about 40 tagged fish in laboratory tanks for several weeks during summer 2008, and no fish lost tags in captivity. In the field, we only captured one Sonora Sucker that had a scar from tagging but that did not contain a tag. We did not observe any direct tagging mortality, and tagging efficacy for small-bodied fish appears to be high (Skov et al. 2005), with negligible effects on movement or survival.

We used a portable antenna system to scan habitats for tagged fish. Our portable unit consisted of a high-performance, low-frequency backpack RFID reader–data-logger with slim antenna tuner board (Oregon RFID, Portland, Oregon) enclosed in a custom-fabricated aluminum waterproof antenna housing with a 2.5-m fiberglass pole (See Supplementary Figure S.1 in Supplement A in the online version of this article). The read range was approximately 50–80 cm, depending on the orientation of the fish and the tag it contained. As tags were detected, tag information was displayed on a ruggedized palm computer (Meazura MEZ1000; Aceeca International, Christchurch, New Zealand) connected via a Bluetooth wireless serial adapter. We recorded the habitat location and detection time for each tag. High densities of tagged fish can result in detections at a higher rate than can be displayed on the palm computer, although all detections are still recorded on the internal data logger. All records were cross-checked with the information in the internal data logger to ensure that we had a complete data set. In general, water clarity was sufficient to enable us to observe fish in water shallower than 0.5 m, so we restricted our search with the portable antenna to deeper water (>0.5 m) and all areas with overhead cover (e.g., roots, undercut banks) regardless of depth. For nearly all habitat scans, the antenna was submerged and placed as deeply beneath overhead cover as possible.

Once each season, we tested our ability to detect tags in the field. Prior to a weekly survey, a colleague hid 10 and 20 tags in locations that would normally be searched under the criteria listed above (in debris piles or deep water) and the survey proceeded as usual. The searcher knew the number but not the locations of hidden tags. After the survey was complete, the number of hidden tags detected was tabulated and those tags were removed from the reach.

From June 3 to August 4, 2008, we collected fish position data within the 1.8-km tagging reach using the portable antenna system ($N = 9$ dates) and conducted physical recaptures (hoop or fyke nets and electrofishing) in nine pool habitats ($N = 9$). From May 18 to July 31, 2009 (portable antenna: $N = 12$; physical recaptures: $N = 7$), and from June 2 to July 1, 2010 (portable antenna: $N = 5$; physical recaptures: $N = 4$), our weekly sampling included the expanded reach 1.3 km downstream and 1 km upstream of the tagging reach (hereafter, the "full reach") to determine whether any animals had moved out of the tagging reach. A concurrent study in 2009 and 2010 (further described in Booth et al. 2013) deployed a series of eight full-stream-width stationary PIT antennas installed in the center of the tagging reach (approximately 25 m apart) and continuously recorded small-scale movements over a 200–300-m reach that included one to two large refuge habitats. In addition, once each in 2009 and 2010, we looked for fish outside of the full reach; as part of the long-term monitoring program of New Mexico Department of Game and Fish, we scanned physically captured fish (electroshocking) for PIT tags in a section 1.3 km downstream of the full reach and used the portable antenna to scan an additional 1.3 km upstream of the full reach to look for fish that moved up the Middle Fork and West Fork of the Gila River.

For all surveys, we began at the downstream end of the reach and worked upstream. Under clear water conditions, the surveys were completed within 5–8 h, but more extensive search efforts (up to 10 h) were necessary when water was turbid. (Sampling was less effective in turbid water because fish were not concentrated in refuge habitats but distributed throughout the stream; Booth et al. 2013). The nature of the search efforts (i.e., placing the antenna beneath overhead cover) typically disturbed the fish within each habitat, but we rarely observed (visually or via the stationary antenna array) fish leaving the habitat being scanned during our searches. Because fish were typically disturbed by the presence of the portable antenna, we were able to determine that tags were still contained in live fish if the tag moved within the habitat. During our surveys, we noted when a tag appeared to have been dropped (as a result of being shed or owing to a fish's dying) based on the following criteria: (1) a tag was detected multiple times in the same location within a habitat and did not move when the area was gently disturbed, or (2) a tag was not detected in the concurrent study using stationary antennas despite remaining within the antenna's reach during the entire season (i.e., the tag was stationary).

Movement analyses.—To measure distances on our GIS map, we overlaid the wetted area of the stream with a 5-m × 5-m grid of equally spaced points and created a distance network of lines that connected the grid points with the center points of fish habitat units. Using the built-in Manifold 8.0 function "Select shortest path," we measured the minimum distances between points (constrained to paths within the wetted region of the stream).

For each individual and year with at least three observations, we calculated the mean movement distance (mean linear displacement between successive detection locations) and home range (maximum linear displacement and total area used by the fish). Upstream movements were assigned positive values and downstream movements negative values (hereafter, "signed movements"). Unsigned movements were the absolute values of the movement distances. Maximum linear displacement was measured as the distance between the two most distant detection locations within the individual fish's record, calculated as above. We calculated home range area using a linear buffer approach. Using all of the detection locations for an individual during each sampling season as well as in all years of the study, we buffered all movement paths and points in Manifold with a 25-m buffer width to create a polygon that included all detection locations and completely overlapped all of the wetted streambed. Because the stream channel varied in width, the buffer polygons necessarily included substantial riparian habitat which cannot be used by fish. To correct these home range estimations, we trimmed the buffer polygons using the wetted stream layer and discarded habitat outside of the wetted area of the stream. All detections of individual fish (including physical recaptures) were included in the calculation of summary statistics, but when comparing movement rates (m/d), we only used data collected from portable telemetry surveys that incorporated the entire study reach to ensure that all segments of the study reach were represented. As recommended by Rodríguez (2002), we report movement metrics for the population as a whole as well as for the mobile and stationary fractions.

We classified habitats as "major" if more than 10 tagged individuals were typically observed in that location and "minor" if fish were rarely detected in the location or few individuals were detected in that habitat. Major habitats were primarily large, deep (>1 m) pools with substantial overhead cover (undercut banks, woody debris, and overhead vegetation), while minor habitats had limited overhead cover and were typically shallow (<0.5 m) but still provided limited hiding places for fish.

We measured growth rates for all fish that were physically recaptured (Sonora Suckers: $N = 66$; Desert Suckers: $N = 3$). In analyses comparing movement metrics with fish size, we estimated growth for fish that were not physically recaptured by fitting a modified von Bertalanffy growth curve to yearly standard length (SL) growth data for those Sonora Suckers we did capture (Fabens 1965) and used the growth model to estimate SL for fish (both species) that were not physically recaptured. If the last measured or estimated SL was greater than our calculated L_∞ (the average maximum SL for the population), we used the last measured SL. We binned the fish into three size-classes based on natural breaks in the data and the fitted maximum size (Sonora Suckers: <230, 230–350, and >350 mm; Desert Suckers: <170, 170–230, and >230 mm). Because our sample size was not adequate to fit a von Bertalanffy growth curve for Desert Suckers, we used the Sonora Sucker curve to estimate growth for that species as well.

Statistical Tests

To assess whether time since release was related to home range, we used analysis of variance (ANOVA) to test the relationship between the total distance moved and the number of days at large. We fit von Bertalanffy growth curves using the nonlinear fit function in JMP (SAS Institute, Cary, North Carolina). We tested whether directionality of movement varied by year and species using ANOVA. For each sampling date, we tested whether the mean directionality of movement was different from zero using the nonparametric Wilcoxon signed rank test. For individuals detected more than two times within a year as well as among years, we assessed whether home range was different within summers vis-à-vis between years using a paired two-sided *t*-test. We used ANOVA with a post hoc Tukey–Kramer honestly significantly different (HSD) test to test for differences in maximum linear displacement and home range among the years of our study. We used a nominal logistic regression with an effect likelihood ratio test to compare size-class with the consistency of movement behavior among years for each individual. We used a chi-square contingency analysis to test for differences in the use of major and minor habitats among years.

Determining the effect of sample size on movement parameters.—Using our data set for Sonora Suckers, we took a replicated-subset approach to estimate how sample size influenced the estimation of movement parameters. We created a custom script in JMP 8.0 to iteratively create random replicated ($N = 1{,}000$) subsets of our overall data set for sample sizes ranging from 5 to 100 or 150 individuals depending on the year; the maximum subset size for each year was at least 20 individuals fewer than the number of individuals in the full data set. For each random subset, we found the maximum values of the mean unsigned movement and maximum linear displacement. To assess the degree to which movement parameters were underestimated for Sonora Suckers, we compared the mean result of all replicates at a particular sample size with the value from the complete data set. We fit linear models of unsigned movement and maximum linear displacement to log-transformed sample size and used analysis of covariance (ANCOVA) to assess the differences in slope among years. Because our sample sizes for Desert Suckers were typically low, we projected the expected maximum values for larger sample sizes using the fitted logarithmic regression equation from Sonora Suckers from the same year.

RESULTS

Detection

Detection was high both for hidden tags and marked fish. Over the 3 years of this study, we typically detected 80–90% of the hidden tags. Detection of live fish was lower than that of hidden tags; comparison of data from the portable antenna with that from stationary antennas in the same habitat indicate detection rates of 50–70%. Of the 430 Sonora Suckers and 119 Desert Suckers tagged, over the course of the study we detected 92% of the Sonora Suckers and 79% of the Desert Suckers at least once, 75% of the Sonora Suckers and 50% of the Desert Suckers 3 or more times, 63% of the Sonora Suckers and 29% of the Desert Suckers 5 or more times, and 31% of the Sonora Suckers and 8% of the Desert Suckers on 10 or more occasions. We observed 29 shed tags (from either live or deceased fish) during the study (8 Sonora Suckers in 2008, 12 in 2009, and 3 in 2010; 4 Desert Suckers in 2008, 1 in 2009, and 1 in 2010).

Movement Analyses

In 2008 and 2009, more than 75% of individuals of both species were observed in two or more locations within each year (range: 1–7 for Sonora Suckers, 1–6 for Desert Suckers). In 2010, 25% of Sonora Suckers and 50% of Desert Suckers were observed in two or more habitats. Although there was a significant correlation between the distance moved and the number of days at large (the time between tagging and resighting) for 2008 ($R^2 = 0.1$, $P < 0.0001$), 2009 ($R^2 = 0.007$, $P = 0.0004$), and 2010 ($R^2 = 0.03$, $P = 0.002$), none of the relationships had useful explanatory power. Yearly growth rates (2009 and 2010 data were pooled due to the small sample size) ranged from 0 to 80 mm SL/year and were strongly size dependent ($R^2 = 0.73$, $F_{1,64} = 176.91$. $P < 0.0001$; von Bertalanffy coefficients: $L_\infty = 381$, $k = 0.0007$; Figure 2). We did not observe any measurable growth within summer seasons, suggesting that the majority of growth occurs during the rest of the year. If the annual growth that we observed were evenly distributed throughout the year, summer growth rates would be within the detection ability of our methods.

The median individual unsigned movement distance was 130 m in 2008 ($N = 167$), 57 in 2009 ($N = 284$), and 59 in 2010 ($N = 120$) for Sonora Suckers and 134 in 2008 ($N = 37$), 59 in 2009 ($N = 43$), and 150 in 2010 ($N = 13$) for Desert Suckers. Overall, there was no upstream or downstream directionality of movement in any year for either species (Table 2; Figure 3). However, there was significant ($P < 0.05$) downstream directionality (often observed after major fish collection efforts within the study reach) on the descending limb of high-flow events and during minimum-flow periods on some dates in 2008, 2009, and 2010 (Figure 4). Up to 24% of Sonora Sucker and 15% of Desert Sucker individuals were detected only in their original tagging locations (Table 2), while up to 41% of Sonora Suckers and 28% of Desert Suckers were observed in locations outside of their original tagging habitat segment but returned to that habitat before the end of the season. Many individuals were detected in the same habitat segment as their last known location during the previous year. Sonora Suckers moved farther between years than within years (paired two-sided *t*-test; 2008–2009 data: $t = 3.125$, df = 131, $P = 0.002$; 2009–2010 data: $t = 2.012$, df = 110, $P = 0.047$), but Desert Suckers did not show this difference (Figure 5).

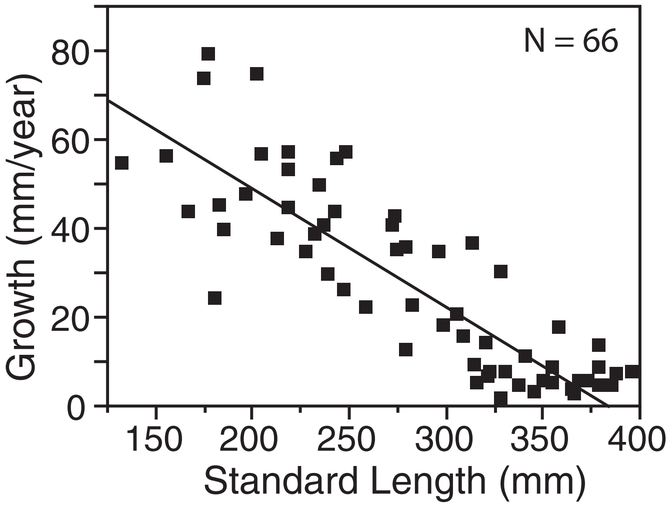

FIGURE 2. Yearly growth rate as a function of body size (initial standard length) for Sonora Suckers. Growth rate = $-0.266 \times \mathrm{SL} + 102.234$; $R^2 = 0.73$, $P < 0.0001$. The von Bertalanffy growth parameters are as follows: $L_\infty = 381$; $k = 0.0007$.

The median maximum linear displacement ranged from 116 to 308 m for Sonora Suckers and from 165 to 600 m for Desert Suckers among the years of the study (Table 3; Figure 6). The maximum linear displacement was smaller for Sonora Suckers in 2010 than in 2008 or 2009 (Tukey–Kramer HSD $q^* = 2.350$; 2008–2010: $P = 0.039$; 2009–2010: $P = 0.023$). Home range (Table 3) followed a similar pattern, with smaller home ranges in 2010 than in 2009 but no difference between 2008 and either year (Tukey–Kramer HSD $q^* = 2.34987$; 2008–2009: $P = 0.8199$; 2008–2010: $P = 0.1606$; 2009–2010: $P = 0.0297$). Desert Suckers did not show any differences in maximum linear displacement or home range among the years of our study.

We classified individuals as stationary if they were only detected in a single location during a season and mobile if they were observed in at least two locations during a season. Individuals did not appear to be of distinct stationary or mobile

TABLE 2. Summary statistics for Sonora Suckers and Desert Suckers with different movement behaviors within years. Positive signed movements indicate upstream travel and negative signed movements downstream travel. Unsigned movement is the absolute value of the total distance moved regardless of direction. These statistics only include fish observed at least twice after release.

	Stationary[a]		Zero net movement[b]			Signed movement					Unsigned movement		
Year and species	*N*	% of total	*N*	Mean ± SE	Range	*N*[c]	Mean ± SE	Median	Maximum downstream	Maximum upstream	Mean ± SE	Median	Range
2008													
Sonora Sucker	32	19%	56	64 ± 20	(0–760)	135	26 ± 19	0	−935	845	253 ± 22	182	(2–1,199)
Desert Sucker	3	8%	6	47 ± 36	(0–226)	34	33 ± 50	2	−731	785	257 ± 43	146	(8–905)
2009													
Sonora Sucker	68	24%	116	59 ± 11	(0–631)	216	4 ± 14	0	−1,100	1,453	186 ± 18	106	(2–2,215)
Desert Sucker	5	12%	12	29 ± 11	(0–112)	38	−64 ± 49	−23	−752	1,310	188 ± 43	70	(10–1,310)
2010													
Sonora Sucker	28	23%	45	58 ± 25	(0–1,079)	92	−7 ± 27	0	−879	1,073	206 ± 34	83	(11–1,799)
Desert Sucker	2	15%	2	0		11	−2 ± 90	22	−472	706	411 ± 125	296	(42–1,328)

[a] Fish that were not observed to move from their tagging location and are not included in the signed and unsigned movement statistics.

[b] Subset of fish that moved but returned to their original location; these individuals are included in the signed and unsigned movement statistics.

[c] *N* includes zero net movement fish.

"morphotypes." However, 57% ($N = 97$) of Sonora Suckers were classified as mobile in all of the years in which they were detected, 9% ($N = 15$) were consistently stationary, and 34% ($N = 58$) exhibited both behaviors over the course of our study. Initial fish size influenced the consistency of behavior (likelihood ratio $\chi^2 = 10.101$, $P = 0.0388$), with more large fish ($\geq$230 mm SL) consistently exhibiting mobile behavior. More small fish exhibited both behaviors than larger fish, though there

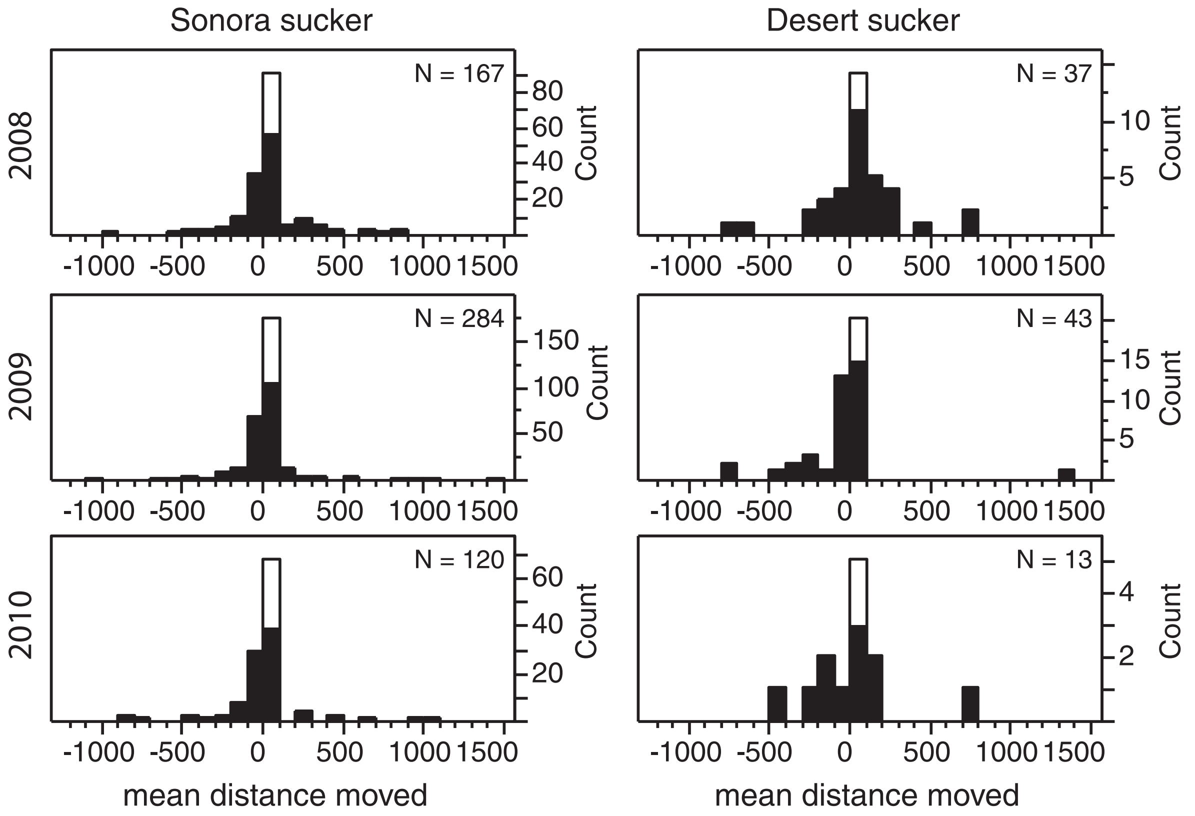

FIGURE 3. Mean movements (m) upstream (positive values) and downstream (negative values) by Sonora Suckers and Desert Suckers. Black bars indicate individuals that were detected outside of their initial tagging location, white bars individuals that were detected only within a single habitat. Data are shown only for individuals that were detected at least twice during the sampling period. Note that the scale of the *y*-axis differs among panels.

TABLE 3. Mean movement distance, maximum linear displacement, home range area, and parameters for statistical tests for tagged Sonora Suckers and Desert Suckers observed two or more times per year in the Gila River. Median values are grouped into all fish (the complete monitored population), mobile fish (>0 maximum linear displacement), and stationary fish (no movement detected).

	2008			2009			2010			*F*	*P*	*q**	*P*		
Variable	All	Mobile	Stationary	All	Mobile	Stationary	All	Mobile	Stationary	All	All	All	2008–2009	2009–2010	2008–2010
							Sonora Suckers								
N	167	135	32	284	216	68	120	92	28						
Mean movement distance (m)	130	182	0	58	106	0	60	83	0	3.18	0.04	2.35	0.033*	0.828	0.286
Maximum linear displacement (m)	308	527	0	181	344	0	116	168	0	3.99	0.02	2.35	0.999	0.023*	0.039*
Home range area (m^2)	4,292	7,378	565	2,896	5,188	641	2,319	3,169	565	3.28	0.04	2.35	0.820	0.030*	0.161
							Desert Suckers								
N	37	34	3	43	38	5	13	11	2						
Mean movement distance (m)	135	146	0	60	70	0	150	296	0	2.22	0.11	2.38	0.503	0.105	0.435
Maximum linear displacement (m)	528	563	0	165	179	0	600	634	0	0.52	0.60	2.38	0.742	0.639	0.925
Home range area (m^2)	7,379	7,665	680	2,333	3,397	609	8,335	8,791	622	0.22	0.80	2.38	0.997	0.819	0.798

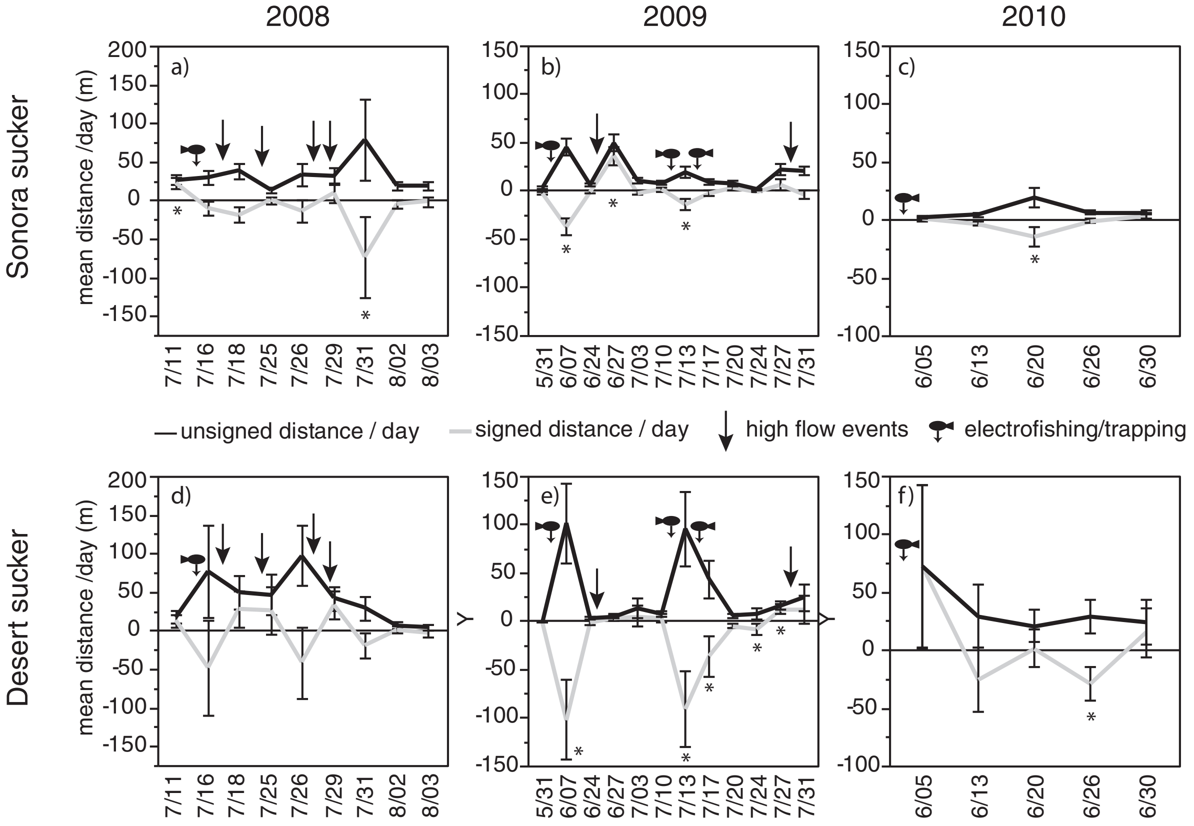

FIGURE 4. Movement rates observed during telemetry surveys. The unsigned movement distance is the absolute value of the distance moved regardless of direction; the signed movement distance is the distance moved upstream (positive values) or downstream (negative values). The error bars represent SEs. Asterisks indicate dates on which the average movement rate was significantly ($P < 0.05$) different from zero (i.e., there was net directionality upstream or downstream). Note that the dates are not evenly spaced along the *x*-axes.

was not a consistent shift in behavior as fish grew. No large Sonora Suckers (>350 mm SL) were consistently stationary. For Desert Suckers, 76% ($N = 13$) were always mobile, 6% ($N = 1$) were consistently stationary, and 18% ($N = 3$) were classified as both. We did not have sufficient numbers of Desert Suckers to test the influence of size on movement behavior.

Although some fish were classified as stationary (individuals detected at single locations only; Table 2), the concurrent effort with stationary antennas in 2009 and 2010 showed that even those fish made regular sojourns outside of the pools where they were detected by means of portable telemetry. The durations of these movements were shorter than those between subsequent portable telemetry surveys (hours to days). In 2009 and 2010, we observed 31 and 21 "stationary" Sonora Suckers and 1 and 2 Desert Suckers, respectively, undertaking movements of at least 25 m outside the habitat where they were observed.

The proportions of observed movements between major and minor habitats were different among the years for Sonora Suckers ($\chi^2 = 111.1$, df = 6, $P < 0.0001$), but not for Desert Suckers ($\chi^2 = 6.08$, df = 6, $P = 0.414$). In 2010, Sonora Sucker

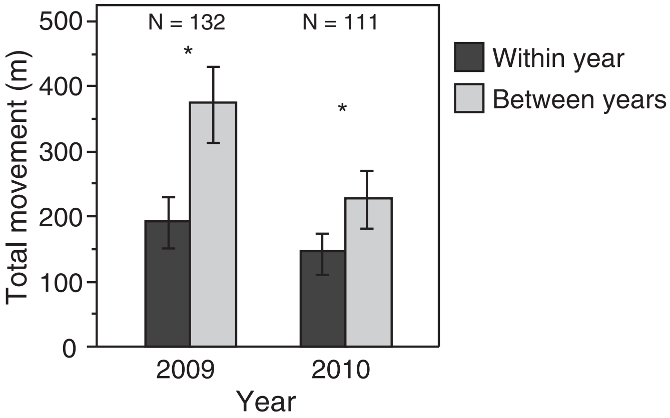

FIGURE 5. Observed movements of Sonora Suckers within and between years. Within-year movements were calculated as the absolute values of the sums of all signed movements for an individual; between-year movements were calculated as the distances between the last observed location in the previous year and the first observed location in the year indicated on the graph. Asterisks indicate significant differences ($P < 0.05$) between within- and between-year movements.

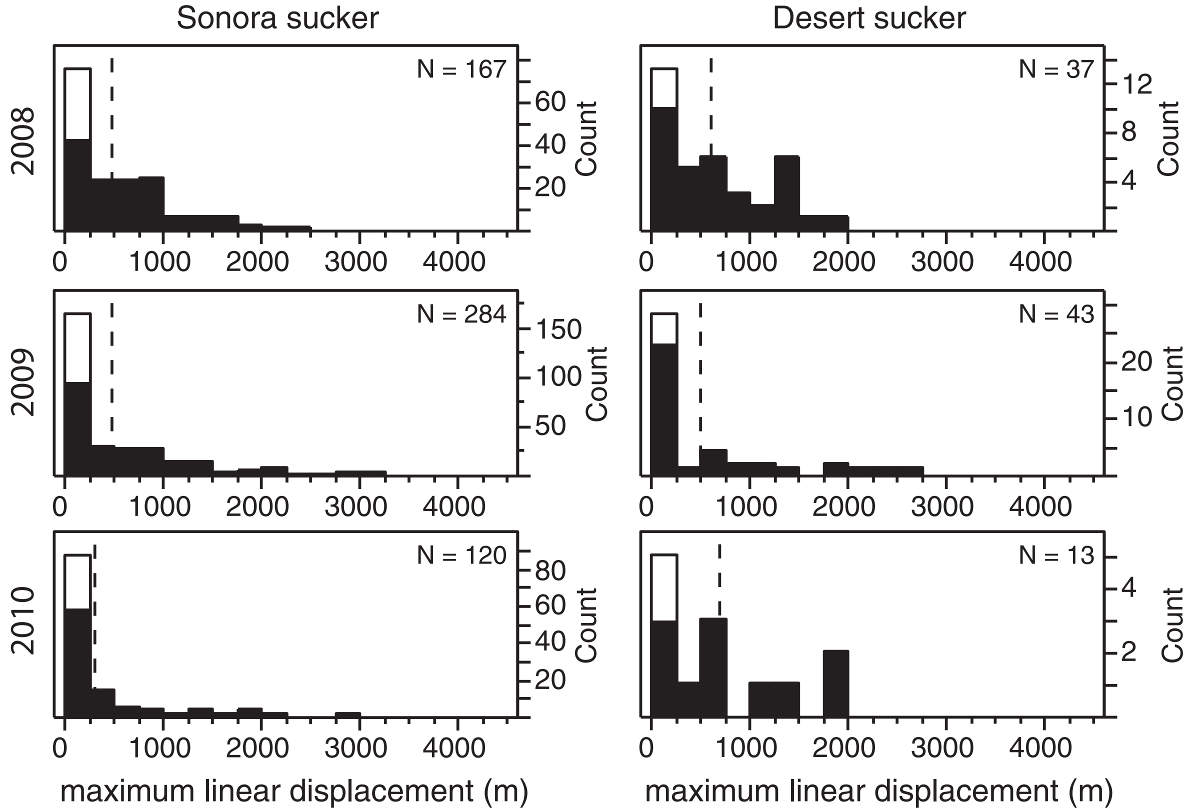

FIGURE 6. Maximum linear displacement (home range) for Sonora Suckers and Desert Suckers. Black bars indicate individuals that were detected outside of their initial tagging locations, white bars individuals that were detected only within a single habitat. Data are shown only for individuals that were detected at least twice during the sampling period. Note that the scale of the *y*-axis differs among panels.

movements were among or into minor habitats and indicated greater use of such habitats than in previous years. Periods of higher flow typically increased the proportion of fish observed in minor habitats, although Desert Suckers were also predominantly found in minor habitats immediately following major electroshocking surveys in early June 2009 and 2010.

There was one substantial flood in the 2009 season (discharge increased from a base flow of about 0.4 m^3/s to more than 5 m^3/s within 10–20 min). We conducted a similar number of telemetry surveys before and after the flood. We observed 204 Sonora Suckers and 18 Desert Suckers prior to the flood event and 238 and 22 after the flood. Of the fish observed postflood, 44 Sonora Suckers and 4 Desert Suckers had not been detected in the reach prior to the flood during 2009. Ten Sonora Suckers were observed prior to the flood but not observed again within the reach during 2009. Only one of the fish that was not detected after the flood was seen again in the 2010 season.

Although we sampled a broad range of sizes (Table 1) of both species, we did not observe any relationship between standard length and any movement metric (mean movement distance, home range, maximum linear displacement, or directionality). We also did not observe any correlation between growth rate or body condition (Fulton's condition factor; Bolger and Connolly 1989) and our movement metrics.

Effect of Sample Size on Movement Parameters

For Sonora Suckers, we found that the maximum mean distance for subsets of movement records with a sample size of 150 represented 97–98% (2008 and 2009) of the known maximum distance for the complete data set and that a subset size of 100 represented 96% (2010). We observed a rapid increase in the population's maximum values for linear displacement and mean distance as increasingly larger subsets of data were included in the analysis up to subsets containing 75–100 individuals, beyond which our estimates approached the values observed in the complete data set (Figure 7). The median values for the mean movement distance were slightly inflated at low sample sizes but rapidly converged to the median for the full data set when the sample size exceeded 30 individuals. A small survey of recent radiotelemetry studies ($N = 15$; see Supplementary Table S.1 in Supplement A) suggests that the typical number of individuals tracked is about 20 (range, 3–43). Using a subset size of 20 individuals in our analyses, the maximum linear displacement was underestimated by 28–35% and the maximum mean distance by 28–62% compared with the values obtained from the complete data set for each year, while the median

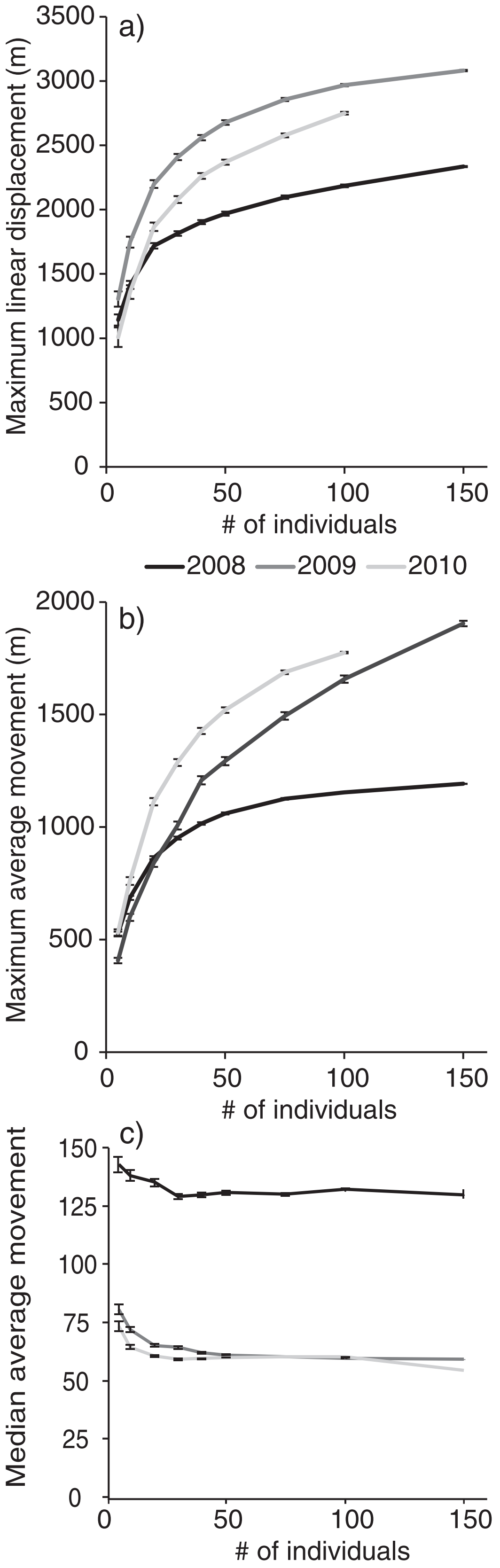

FIGURE 7. **(a)** Maximum linear displacement, **(b)** maximum mean movement, and **(c)** median mean movement of Sonora Suckers estimated using increasing subsets of sample data by study year. The standard errors (error bars) are small relative to the scale of the axis and are largely masked by the trend line. The data represent 1,000 random draws of individuals from the total pool per subset size.

mean distance was similar to that from the complete data set. The slopes of the accumulation curves (Figure 7) differed significantly among years (ANCOVA of log-transformed sample size; maximum linear displacement: $F_{5,\,26{,}994} = 7{,}592.27$, $P < 0.00001$; maximum mean distance: $F_{5,\,26{,}994} = 5{,}709.15$, $P < 0.00001$) and was greater in 2009 and 2010 than 2008. In other words, fewer fish were needed in 2008 to describe the range of these movement parameters than in 2009 or 2010.

DISCUSSION

The patterns of movement by two ecologically significant species of catostomid fish native to streams of the southwestern United States varied markedly in the Gila River from year to year as well as among individuals. Although we have less robust data for Desert Suckers, for both species we observed a relatively high proportion of individuals exhibiting both mobile and sedentary behaviors for extended periods, providing evidence that movement behavior is not fixed for an individual, even within a particular life stage. We expected that individual movement might respond coherently to changes in the abiotic environment (e.g., floods; Harvey et al. 1999) as well as attributes of the fish (e.g., size; Schrank and Rahel 2006), but abiotic environmental conditions did not appear to influence movement patterns in a consistent way within or among years.

The majority of the individuals sampled made relatively large movements within the summer season as well as from one summer to the next. Proportionally more Sonora Suckers than Desert Suckers were stationary and found repeatedly (exclusively or nearly exclusively) in single locations (consistent with other work with these species; Booth and Shipley 2012). But in general, Sonora Suckers and Desert Suckers did not differ significantly in their movement parameters. Other studies have shown that fishes with differing diets and microhabitat preferences tend to have different movement dynamics (e.g., Brown Trout *Salmo trutta* and White Sucker *Catostomus commersonii*: Brown et al. 2001; Hitch *Lavinia exilicauda* and Sacramento Sucker *C. occidentalis*: Jeffres et al. 2006). Previous accounts (Minckley and Marsh 2009) describe Sonora and Desert Suckers as having different food and habitat preferences, but our observations suggest that these species do not differ from each other with respect to microhabitat preferences in the Gila River (adults of both species regularly co-occurred in most habitats). The degree to which Sonora Sucker and Desert Sucker diets overlap (ranging from invertivore and herbivore, respectively, to facultative omnivores) appears to be variable among streams and seasons (Schreiber and Minckley 1981; Clarkson and Minckley 1988; Pilger et al. 2010), and the diet overlap observed in the Gila River (Pilger et al. 2010) may be partially a result of similar movement behavior.

Patterns of sustained displacement among habitats over a relatively large spatial scale (>1 km) may result from the aggregation of multiple small individual movements over an extended time period or from a single continuous movement. Concurrent data (Booth et al. 2013) collected using stationary antennas indicated that both sucker species performed nightly foraging movements from focal refuge sites into adjacent shallow habitats (at least 25–200 m away). Nightly foraging trips are likely to be leptokurtically distributed, i.e., the majority of trips occur relatively close to the refuge habitat due to the variation in exploratory behavior among individuals (Fraser et al. 2001). Short-term forays, like the overnight trips observed among Sonora Suckers and Desert Suckers, may give fish information on the distribution of resources within the stream and lead to the use of alternative refuge sites. Although Booth et al. (2013) observed high fidelity to particular refuge habitats, most individuals made extended forays away from their home habitat. Because we were only able to survey the full reach about once each week, we cannot estimate the extent of typical nightly forays and may have missed displacements at shorter time scales of 1–6 d (Baras 1998; Ovidio et al. 2000), which would lead to underestimates of home range size. Despite these limitations, we observed movements by both species and summer home ranges on the order of kilometers, and we expect that these estimates are robust minimum estimates of fish movements in the Gila River.

Although we thought that changes in discharge might modify the direction or magnitude of movements, neither species consistently moved up- or downstream following flood events. High-flow events in 2008 resulted in net downstream movement, while those of similar magnitude in 2009 resulted in upstream displacement. This may have been due to fish using sheltered refuge habitats during high flows (Harvey et al. 1999) or to their being capable of orienting to high flows to avoid displacement (Meffe 1984). Previous work indicates that the fishes of the Southwest, including Sonora Suckers and Desert Suckers, exhibit behaviors that limit displacement by flood events (Meffe 1984; Rinne and Stefferud 1997; Schultz et al. 2003; Booth and Shipley 2012). The behavioral response of fish to high-flow events and their ability to resist displacement will determine how fish communities are structured over short time periods (Matthews 1986).

Elevated flows, potentially interacting with turbidity levels, increased the proportion of fish using minor (i.e., small, marginal quality) refuge habitats. Minor habitats typically did not provide ample overhead cover or were extremely shallow during low-flow periods. Few individual fish were consistently found in the same minor habitat, indicating that those areas were potentially marginal refuge habitat and used only transiently. However, in 2010 (a high-discharge year), the majority of Sonora Sucker movements were into minor habitats. While major refuge sites may provide high-quality refuge habitat for large numbers of individuals, the use of minor refuges may be advantageous if they give closer access to less frequently available feeding habitats even at the cost of potentially higher predation risk. In high-flow periods, minor habitats may provide sufficient refuge due to decreased visibility from increased water depth and elevated turbidity, but in low-flow periods they are likely to be too risky for consistent use by individuals. Many species of fish show strong associations with discrete habitat patches (Fausch et al. 2002; Belica and Rahel 2008), and conceptual models (Schlosser and Angermeier 1995) show that the typical life cycle of a stream fish consists of movements between refugia and favorable feeding habitats. Variation in refuge quality, both among sites and within a site over time, likely plays an important role in determining the distribution of fishes and their movements among habitats. For example, increasing the complexity of habitat while controlling for habitat size greatly increased the diversity of fish species found in artificial habitat patches in a tropical river (Arrington et al. 2005).

Interestingly, the responses of the fish to floods were of a similar magnitude to the movements coinciding with our collection activities, although sampling-induced movements were typically downstream while the movements immediately following flooding generally had little or no net direction. Unlike studies involving salmonids, which indicate either little movement (Young and Schmetterling 2004) or upstream movement (Peterson et al. 2005), we observed downstream movement following fish collecting activities. We suspect that some of the downstream movements were a return of individuals to their prior habitat—electrofishing efforts downstream appeared to "herd" fish upstream into major habitats, while hoop and fyke nets may have captured visiting individuals during nightly foraging forays. Electrofishing in downstream habitats in 2009 elevated population sizes in upstream habitats (Booth et al. 2013), which then dropped to pre-electroshocking levels within a few days as fish returned downstream. Electrofishing occurred only once per season during our study and likely did not modify movements over the entire season. However, given that many mark–recapture studies rely on electroshocking to capture fish and estimate movement parameters, it is critical to know whether individuals respond to sampling efforts and on what time frames, and whether other taxa show different responses.

In all years of the study, the mean movement distance by suckers in the Gila River was on the order of hundreds of meters, although some individuals of both species were observed to make distinct movements of over a kilometer and had overall displacements of several kilometers. The home ranges for mobile individuals were typically several hundred meters long (measured as maximum linear displacement) and included several distinct refuge habitats. There is evidence that habitat size drives the overall range of fish movement (Woolnough et al. 2009), and we observed greater movement distances by Sonora Suckers and Desert Suckers than did Booth and Shipley (2012) for the same species in streams in Arizona, likely in part because the Gila River is longer and the spatial scale of our study (6 km) larger than is the case with the small streams (hundreds of meters; median discharge, <0.1 m^3/s) that they studied. The movements detected in this study are similar in magnitude to those observed by Siebert (1980) and Williams (1991) but substantially greater than those observed by Bestgen et al. (1987) for Sonora Suckers and Desert Suckers. Unlike Siebert (1980), who found that suckers exhibited a tendency to move into a canyon-bounded reach of Aravaipa Creek during summer, we did not observe directional movements upstream into the canyon-bounded reach of the Middle Fork Gila River. Other species of suckers in larger rivers are highly mobile during nonreproductive periods (Chart and Bergersen 1992; Matheney and Rabeni 1995), and it seems likely that mobility is a characteristic of catostomids in general.

Although we collected movement data over several years, we only collected data during summer, meaning that we have measures within summers and can compare locations of fish from one summer to the next but have no information for other times of year. While we observed movements within and among years, it is possible that Sonora and Desert Suckers also make major spawning movements in spring, when discharge is too high to deploy our telemetry equipment. Related catostomid species are known to perform spawning migrations (Tyus and Karp 1990; Decker and Erman 1992; Modde and Irving 1998; Schmetterling and Mcfee 2006; Compton et al. 2008; Sweet and Hubert 2010), and historical, anecdotal reports from Arizona (Minckley 1973) suggest that the major rivers of the Southwest have experienced large spawning runs of fish, at least in the past. Given that these species are of conservation interest, it will be particularly critical to understand whether these fish make spawning migrations, which would provide a genetic link between up- and downstream populations and enable recolonization of habitats after local extirpation. Previous work found high fidelity by some individuals to our study reach among years (Booth et al. 2013), suggesting that if spawning movements occur many individuals exhibit some level of homing behavior to their summer habitat. Homing behavior has been observed in other benthic fishes in large rivers, although individuals varied in motivation or ability to return to a focal habitat (Crook 2004). The prevalence of homing behavior may vary with environmental conditions, food availability, or behavioral interactions, and similar to plasticity in movement behavior, individuals may change homing behavior depending on the context.

Subset Analysis

Other studies have considered the effects of the timing of sampling surveys (Baras 1998; Ovidio et al. 2000) and the number of detections per individual (Crook 2004) on the estimation of home ranges. However, it remains unclear how estimates of movement parameters at the population level vary based on the number of individuals tracked—probably because there are relatively few data sets containing sufficiently large numbers of fish that were tagged and subsequently detected multiple times. PIT telemetry (e.g., Cucherousset et al. 2005; Bubb et al. 2006; Hill et al. 2006; Enders et al. 2007; Teixeira and Cortes 2007; Johnston et al. 2009) shows great promise for in-depth, long-term studies investigating the variation in movement parameters within populations and through time. We found that the number of individuals included in movement estimates can strongly influence the estimation of population-level parameters, particularly if there is marked variation in behavior among the individuals. Although radiotelemetry has important advantages over other approaches because of its ability to detect long-distance movements as well as to provide high-resolution temporal data (Lucas and Baras 2000), our analysis suggests that the number of individuals typically used in radiotelemetry studies (3–49; Supplementary Table S.1) would almost certainly have led to significant underestimates of both the home range and average maximum movement despite the fact that there is likely an asymptotic relationship between sample size and parameter estimates (Crook 2004). We estimate that a sample size of 75–100 individuals would be required to assure that the full range of individual movement distances observed in our full data set of 431 fish is adequately represented. The required sample size will undoubtedly vary depending on the taxon, site, and environmental conditions, and the degree of variation in movement behavior within taxa will determine the effect of sample size on estimate quality. Based on our subset analysis using our extensive Sonora Sucker data set, it is likely that we have underestimated the movement parameters for Desert Suckers because our data for them are much more limited (the species was relatively uncommon in our study area). This suggests that Desert Suckers are more mobile than the estimates that we report here imply. If we assume that the relationships between sample size and parameter estimates are similar for Desert Suckers and Sonora Suckers within years, the maximum linear displacement for Desert Suckers was likely underestimated by 20–40% (about 375–800 m) and the average maximum movement by 19–49% (about 170–640 m). Underestimates of movement parameters may be particularly problematic when those parameters are used to infer fish production, the size of the habitats necessary to maintain populations, the degree of connectivity among populations (Gowan et al. 1994), and the effects of ecosystem engineering behavior (our unpublished data).

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REFERENCES

Arrington, D. A., K. O. Winemiller, and C. A. Layman. 2005. Community assembly at the patch scale in a species-rich tropical river. Oecologia 144:157–167.

Baras, E. 1998. Selection of optimal positioning intervals in fish tracking: an experimental study on *Barbus barbus*. Hydrobiologia 371/372:19–28.

Belica, L. A. T., and F. J. Rahel. 2008. Movements of Creek Chubs, *Semotilus atromaculatus*, among habitat patches in a plains stream. Ecology of Freshwater Fish 17:258–272.

Bestgen, K., A. Hendrickson, D. Kubly, and D. L. Propst. 1987. Movements and growth of fishes in the Gila River drainage, Arizona and New Mexico. Southwestern Naturalist 32:351–356.

Bolger, T., and P. L. Connolly. 1989. The selection of suitable indices for the measurement and analysis of fish condition. Journal of Fish Biology 34:171–182.

Booth, M. T., N. G. J. Hairston, and A. S. Flecker. 2013. How mobile are fish populations? Diel movement, population turnover, and site fidelity in suckers. Canadian Journal of Fisheries and Aquatic Sciences 70:666–677.

Booth, M. T., and A. Shipley. 2012. Spatial dynamics and growth of two native catostomid species: are movements restricted? Southwestern Naturalist 57:248–256.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393–405.

Brown, R. S., G. Power, and S. Beltaoa. 2001. Winter movements and habitat use of riverine Brown Trout, White Sucker, and Common Carp in relation to flooding and ice break-up. Journal of Fish Biology 59:1126–1141.

Bryant, M. D., M. D. Lukey, J. P. McDonell, R. A. Gubernick, and R. S. Aho. 2009. Seasonal movement of Dolly Varden and Cutthroat Trout with respect to stream discharge in a second-order stream in Southeast Alaska. North American Journal of Fisheries Management 29:1728–1742.

Bubb, D. H., T. J. Thom, and M. C. Lucas. 2006. Movement patterns of the invasive signal crayfish determined by PIT telemetry. Canadian Journal of Zoology 84:1202–1209.

Chart, T. E., and E. P. Bergersen. 1992. Impact of mainstream impoundment on the distribution and movements of the resident Flannelmouth Sucker (Catostomidae: *Catostomus latipinnis*) population in the White River, Colorado. Southwestern Naturalist 37:9–15.

Clarkson, R. W., and W. L. Minckley. 1988. Morphology and foods of Arizona catostomid fishes: *Catostomus insignis, Pantosteus clarki*, and their putative hybrids. Copeia 1988:422–433.

Compton, R. I., W. A. Hubert, F. J. Rahel, M. C. Quist, and M. R. Bower. 2008. Influences of fragmentation on three species of native warmwater fishes in a Colorado River basin headwater stream system, Wyoming. North American Journal of Fisheries Management 28:1733–1743.

Crook, D. A. 2004. Is the home range concept compatible with the movements of two species of lowland river fish? Journal of Animal Ecology 73: 353–366.

Cucherousset, J., J.-M. Roussel, R. Keeler, R. A. Cunjak, and R. Stump. 2005. The use of two new portable 12-mm PIT tag detectors to track small fish in shallow streams. North American Journal of Fisheries Management 25:270–274.

Decker, L. M., and D. C. Erman. 1992. Short-term seasonal changes in composition and abundance of fish in Sagehen Creek, California. Transactions of the American Fisheries Society 121:297–306.

Enders, E. C., K. D. Clarke, C. J. Pennell, L. M. N. Ollerhead, and D. A. Scruton. 2007. Comparison between PIT and radio telemetry to evaluate winter habitat use and activity patterns of juvenile Atlantic Salmon and Brown Trout. Hydrobiologia 582:231–242.

Fabens, A. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:1–16.

Flecker, A. S., P. B. Mcintyre, J. W. Moore, J. T. Anderson, B. W. Taylor, and R. O. Hall. 2010. Migratory fishes as material and process subsidies in riverine ecosystems. Pages 559–592 *in* K. B. Gido and D. A. Jackson, editors.

Community ecology of stream fishes: concepts, approaches, and techniques. American Fisheries Society, Symposium 73, Bethesda, Maryland.

Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. American Naturalist 158:124–35.

Gowan, C., and K. D. Fausch. 1996. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecological Applications 6:931–946.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51:2626–2637.

Harvey, B. C., R. J. Nakamoto, and J. L. White. 1999. Influence of large woody debris and a bankfull flood on movement of adult resident Coastal Cutthroat Trout (*Oncorhynchus clarki*) during fall and winter. Canadian Journal of Fisheries and Aquatic Sciences 56:2161–2166.

Hill, M. S., G. B. Zydlewski, J. D. Zydlewski, and J. M. Gasvoda. 2006. Development and evaluation of portable PIT tag detection units: PITpacks. Fisheries Research 77:102–109.

Jeffres, C. A., A. P. Klimley, J. E. Merz, and J. J. Cech. 2006. Movement of Sacramento Sucker, *Catostomus occidentalis*, and Hitch, *Lavinia exilicauda*, during a spring release of water from Camanche Dam in the Mokelumne River, California. Environmental Biology of Fishes 75:365–373.

Johnston, P., F. Bérubé, and N. E. Bergeron. 2009. Development of a flatbed passive integrated transponder antenna grid for continuous monitoring of fishes in natural streams. Journal of Fish Biology 74:1651–1661.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. J. Stauffer. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh.

Linnansaari, T., J.-M. Roussel, R. Cunjak, and J. Halleraker. 2007. Efficacy and accuracy of portable PIT antennae when locating fish in ice-covered streams. Hydrobiologia 582:281–287.

Lucas, M. C., and É. Baras. 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. Fish and Fisheries 1:283–316.

Matheney, M. P. I., and C. F. Rabeni. 1995. Patterns of movement and habitat use by Northern Hog Suckers in an Ozark stream. Transactions of the American Fisheries Society 124:886–897.

Matthews, W. J. 1986. Fish faunal structure in an Ozark stream: stability, persistence, and a catastrophic flood. Copeia 1986:388–397.

Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator–prey fish species. Ecology 65:1525–1534.

Minckley, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix.

Minckley, W. L., and P. C. Marsh. 2009. Inland fishes of the greater Southwest. University of Arizona Press, Tucson.

Modde, T., and D. B. Irving. 1998. Use of multiple spawning sites and seasonal movement by Razorback Suckers in the Middle Green River, Utah. North American Journal of Fisheries Management 18:318–326.

Mueller, G., P. C. Marsh, G. Knowles, and T. Wolters. 2000. Distribution, movements, and habitat use of Razorback Sucker (*Xyrauchen texanus*) in a lower Colorado River reservoir, Arizona–Nevada. Western North American Naturalist 60:180–187.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal research. Proceedings of the National Academy of Sciences of the USA 105:19052–19059.

Ovidio, M., J. Philippart, and É. Baras. 2000. Methodological bias in home range and mobility estimates when locating radio-tagged trout, *Salmo trutta*, at different time intervals. Aquatic Living Resources 13:449–454.

Peterson, J., N. Banish, and R. Thurow. 2005. Are block nets necessary? Movement of stream-dwelling salmonids in response to three common survey methods. North American Journal of Fisheries Management 25:732–743.

Pilger, T. J., K. B. Gido, and D. L. Propst. 2010. Diet and trophic niche overlap of native and nonnative fishes in the Gila River, USA: implications for native fish conservation. Ecology of Freshwater Fish 19:300–321.

Rinne, J. N., and D. Miller. 2006. Hydrology, geomorphology, and management: implications for sustainability of native Southwestern fishes. Reviews in Fisheries Science 14:91–110.

Rinne, J. N., and J. A. Stefferud. 1997. Factors contributing to collapse yet maintenance of a native fish community in the desert Southwest (USA). Pages 157–162 *in* D. A. Hancock, D. C. Smith, A. Grant, and J. P. Beumer, editors. Developing and sustaining world fisheries resources: the state of science and management. Proceedings of the 2nd World Fisheries Congress. World Fisheries Congress, Brisbane, Australia.

Rodríguez, M. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83:1–13.

Roussel, J. M., A. Haro, and R. A. Cunjak. 2000. Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. Canadian Journal of Fisheries and Aquatic Sciences 57:1326–1329.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Schmetterling, D. A., and J. A. Mcfee. 2006. Migrations by fluvial Largescale Suckers (*Catostomus macrocheilus*) after transport upstream of Milltown Dam, Montana. Northwest Science 80:18–25.

Schrank, A. J., and F. J. Rahel. 2006. Factors influencing summer movement patterns of Bonneville Cutthroat Trout (*Oncorhynchus clarkii utah*). Canadian Journal of Fisheries and Aquatic Sciences 63:660–669.

Schreiber, D. C., and W. L. Minckley. 1981. Feeding interrelations of native fishes in a Sonoran desert stream. Great Basin Naturalist 41:409–426.

Schultz, A. A., O. E. Maughan, S. A. Bonar, and W. J. Matter. 2003. Effects of flooding on abundance of native and nonnative fishes downstream from a small impoundment. North American Journal of Fisheries Management 23:503–511.

Siebert, D. J. 1980. Movement of fishes in Aravaipa Creek, Arizona. Master's thesis. Arizona State University, Tempe.

Skalski, G. T., and J. F. Gilliam. 2003. A diffusion-based theory of organism dispersal in heterogeneous populations. American Naturalist 161:441–458.

Skov, C., J. Brodersen, C. Brönmark, L. A. Hansson, P. Hertonsson, and P. A. Nilsson. 2005. Evaluation of PIT-tagging in cyprinids. Journal of Fish Biology 67:1195–1201.

Sublette, J. E., M. D. Hatch, and M. Sublette. 1990. The fishes of New Mexico. University of New Mexico Press, Albuquerque.

Sweet, D. E., and W. A. Hubert. 2010. Seasonal movements of native and introduced catostomids in the Big Sandy River, Wyoming. Southwestern Naturalist 55:382–389.

Teixeira, A., and R. Cortes. 2007. PIT telemetry as a method to study the habitat requirements of fish populations: application to native and stocked trout movements. Hydrobiologia 582:171–185.

Tyus, H. M., and C. A. Karp. 1990. Spawning and movements of Razorback Sucker, *Xyrauchen texanus*, in the Green River basin of Colorado and Utah. Southwestern Naturalist 35:427–433.

Williams, C. M. 1991. Fish movement relative to physical environment in a Sonoran Desert stream. Master's thesis. Arizona State University, Tempe.

Woolnough, D. A., J. A. Downing, and T. J. Newton. 2009. Fish movement and habitat use depends on water body size and shape. Ecology of Freshwater Fish 18:83–91.

Young, M. K. 2011. Generation-scale movement patterns of Cutthroat Trout (*Oncorhynchus clarkii pleuriticus*) in a stream network. Canadian Journal of Fisheries and Aquatic Sciences 68:941–951.

Young, M., and D. Schmetterling. 2004. Electrofishing and salmonid movement: reciprocal effects in two small montane streams. Journal of Fish Biology 64:750–761.

Zydlewski, G. B., G. Horton, T. Dubreuil, B. Letcher, S. Casey, and J. D. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. Fisheries 31:492–502.