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How mobile are fish populations? Diel movement, population turnover, and site fidelity in suckers

Michael T. Booth, Nelson G. Hairston, Jr., and Alexander S. Flecker

Abstract: Movement of organisms is an important mechanism controlling an array of processes within ecosystems. Recent analyses suggest that movement is composed of individual displacement (distance moved by individuals) and turnover (proportion of individuals moving). Turnover of individuals is important because it influences population size and structure, as well as interactions among individuals and different species within a habitat. We used stationary antennas and passive integrated transponders tags to monitor individual habitat use, turnover, and displacement of Sonora suckers (*Catostomus insignis*) and desert suckers (*Catostomus clarkii*) in the West Fork Gila River, New Mexico, USA. Many tagged fish used our focal stationary antenna reach, but only a subset was consistently present. Population size and turnover rates were variable from day to day. Although some individuals spent the majority of their time within the focal reach, most made extended departures (one or more days) from their home pools. Many individuals displayed fidelity to a particular habitat despite forays elsewhere, returning to the focal reach throughout the study. Diel or short-term movements may explain high turnover rates typically observed and, combined with high site fidelity, may result in the misclassification of individuals as sedentary, despite frequent, potentially short-term, movements into other habitats.

Résumé : Le mouvement d'organismes est un important mécanisme qui régit divers processus au sein des écosystèmes. Des analyses récentes suggèrent que ce mouvement comprend les déplacements individuels (la distance parcourue par des individus) et le roulement (la proportion des individus qui se déplacent). Le roulement est important puisqu'il influence la taille et la structure des populations, ainsi que les interactions entre individus et entre espèces au sein d'un même habitat. Nous avons utilisé des antennes stationnaires et des radio-étiquettes passives intégrées pour surveiller l'utilisation individuelle de l'habitat, le roulement et les déplacements de meuniers *Catostomus insignis* et *Catostomus clarkii* dans la fourche occidentale de la rivière Gila (Nouveau-Mexique, États-Unis). De nombreux poissons étiquetés ont utilisé la zone de portée focale de l'antenne, mais seul un sous-ensemble la fréquentait régulièrement. La taille de la population et le taux de roulement variaient d'une journée à l'autre. Si certains individus passaient la majeure partie de leur temps dans cette zone, la plupart s'absentaient de leurs fosses d'attache pendant de longues périodes (un jour ou plus). De nombreux individus faisaient preuve de fidélité à un habitat particulier, malgré des excursions vers d'autres lieux, revenant à la zone de portée focale tout au long de l'étude. Des mouvements quotidiens ou de courte durée pourraient expliquer les taux de roulement élevés communément observés et, jumelés à une forte fidélité au site, pourraient se traduire par la classification comme sédentaires de certains individus malgré leurs déplacements fréquents, possiblement de courte durée, vers d'autres habitats. [Traduit par la Rédaction]

Introduction

Movement is an important mechanism regulating a variety of characteristics and processes of stream ecosystems, including population dynamics (Nathan et al. 2008; Patterson et al. 2008), predator-prey dynamics (Mitchell and Lima 2002), community structure (Matthews 1998), and habitat requirements (Teixeira and Cortes 2007; Belica and Rahel 2008). Large-scale movements may be required for reproduction, dispersing to new habitats, or avoiding adverse habitat or resource conditions (Bryant et al. 2009; Flecker et al. 2010; Young 2011). Small-scale and short-term movements can provide opportunities for individuals to avoid predation risk or maximize foraging opportunities (Smithson and Johnston 1999; Gowan and Fausch 2002; Belica and Rahel 2008) and are particularly important in heterogeneous ecosystems like streams, where it is possible to access patches of differing quality within relatively small areas. Movement, at both large and small scales, can influence fisheries dynamics in managed systems. For example, if fish regularly move between areas with and without restricted fishing, regulations may be less effective in maintaining

populations (Clapp et al. 1990; Popoff and Neumann 2005). Movement dynamics (e.g., immigration and loss) can be used to assess habitat quality for fish and appear to provide a more reliable assessment of habitat suitability than traditional density-quality relationships (Bélanger and Rodriguez 2002).

Although biologists have recognized that some fishes make diel migrations between habitats (e.g., feeding and refuge areas), studies have typically focused on a few individuals (Young 1999; Crook et al. 2001; David and Closs 2003) or the fish community as a whole with little information on individual behavior (Comeau and Boisclair 1998; Pierce et al. 2001; Arrington and Winemiller 2003). To our knowledge, few, if any, studies have examined diel or small-scale movements for a substantial portion of the fish population with information on individual behavior. Historically, the dominant paradigm of stream fish movement was that adult fish are typically sedentary and occupy a restricted home range (Gerking 1959; Gowan et al. 1994); however, later work suggested that fish populations are often composed of a mixture of sedentary and mobile individuals (Gowan et al. 1994; Rodríguez 2002).

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Recent analyses suggest that population-level movement has two components: displacement (distance moved by individuals) and turnover (proportion of individuals moving) of individuals (Schrank and Rahel 2006). The dynamics of individual turnover deserve more explicit consideration in movement studies, because they influence population size and structure for a particular habitat. High turnover has been assumed to indicate high mobility, but if home ranges are small, many individuals may leave a particular habitat (high turnover) but not move far (Rodríguez 2002). Some individuals may have a primary home habitat (e.g., pool), but make occasional forays into distant locations, while others may consistently move throughout the stream. There is evidence that individuals may exhibit fidelity to a particular habitat (Steingrímsson and Grant 2003), display home range shifts over time (Crook 2004), or have no apparent home range (Linfield 1985). However, more studies are needed to measure the degree to which behavior patterns vary within fish populations or among species, how habitats are used, daily movement patterns and the turnover of individuals within habitats, and how these metrics may change under different environmental conditions. For example, environmental conditions can influence movement behavior in a variety of ways. Floods or spates can cause downstream displacement of individuals (Ward et al. 2003), lateral displacement of fish as they avoid high velocity areas in the main stream channel (Matheney and Rabeni 1995), or provide access to flood plain habitats for foraging (Agostinho and Zalewski 1995). Even for well-studied taxa like salmonids, turnover rates and movement patterns can be variable among individuals and streams (Rodríguez 2002), and it seems likely that more distantly related fishes will show an even broader range of variation. By tracking a large proportion of the individuals within a population, it will be possible to understand the degree to which individuals within populations and species vary in their movement behavior, providing critical data for managing fisheries and developing effective conservation approaches.

Until recently, tracking movements of individuals at a population scale has been difficult — radio telemetry is typically limited in the number of individuals (because of cost, limited signal frequencies, and the logistical challenge of tracking many fish simultaneously), and techniques that require physical recapture (e.g., electroshocking) are limited in the frequency and scale of sampling (Lucas and Baras 2000). Acoustic tags have been shown to address some of these limitations and allow tracking large numbers of individuals in major river systems, but tracking is limited to habitats that provide water depths greater than 3 m, restricting its use to large bodies of water (McMichael et al. 2010). Remote detection of passive integrated transponder (PIT) tags allow low cost, long-term monitoring of movement patterns of large numbers of organisms within small stream ecosystems (Zydlewski et al. 2001, 2006). Developments in PIT telemetry such as portable and stationary in situ antennas allow investigation of fish behavior at high resolution over small spatial and temporal scales for large numbers of individuals (Roussel et al. 2004; Linnansaari et al. 2007; Breen et al. 2009). Depending on the antenna design and deployment, it is possible to address questions such as fish passage through barriers (Compton et al. 2008), microhabitat use (Teixeira and Cortes 2007; Johnston et al. 2009), site visitation frequency (McCormick and Smith 2004), as well as migratory behavior (Zydlewski et al. 2006).

Movements between refuge and foraging habitats may be common in aquatic systems (Burke 1995; Harvey and Nakamoto 1999; Meyer et al. 2000), but have not been investigated for many taxa. Refuge habitats typically provide animals with lower risk of predation, but often at the cost of lost feeding opportunities (Krause et al. 1998), although in some instances the structure providing refuge (e.g., submerged aquatic vegetation) also offers increased foraging opportunities (Rozas and Odum 1988). The timing, frequency, and distance that an animal moves between refuge and

foraging habitats must take into account predation risk, which is often size-dependent (Krause et al. 1998). Better understanding of the variation in small-scale movements and particularly movements among refuge sites may help elucidate the processes and individual characteristics that control this trade-off.

Movement provides important linkages among populations and habitats, and there is a strong need to understand how native species move within the landscape to conserve appropriate habitat to maintain local populations and fisheries as a whole. The movement patterns of many common fishes in the American Southwest are poorly understood (Bestgen et al. 1987), although there is a substantial body of literature for endangered taxa like the razorback sucker (*Xyrauchen texanus*; Tyus and Karp 1990; Modde and Irving 1998; Mueller et al. 2000; Zelasko et al. 2010). To understand small-scale movements and population turnover, we focused on two common, large-bodied fish in southwestern US streams: the Sonora sucker (*Catostomus insignis*) and desert sucker (*Catostomus clarkii*). In this study we used PIT telemetry to study the diel behavior and habitat use by resident fish in a stream, directly estimated population turnover rates within a habitat over time, and assessed whether individuals exhibit day-to-day fidelity to a particular habitat during the summer season. We also used our data to investigate changes in individual behavior due to hydrologic changes (low flow and spates) and between years.

Methods

Study species

Members of the family Catostomidae (suckers) are often the most abundant large-bodied native fish in southwestern streams. *Catostomus insignis* and *C. clarkii* occur in a broad range of streams in Arizona and New Mexico, ranging from the subalpine White Mountains to the Sonoran Desert (Minckley 1973). *Catostomus insignis* feeds on invertebrates and detritus (Schreiber and Minckley 1981) and is abundant in deep pools with restricted flow and fine substrates (Minckley 1973), where it is often found in large aggregations (>30 individuals). In contrast, *C. clarkii* is an algivore that generally scrapes algae off hard substrates. Small *C. clarkii* (50 mm standard length) show continuous feeding with crepuscular peaks (Fisher et al. 1981), and anecdotal evidence suggests that adult suckers of both species use pool margins and riffles during the evening (Minckley and Marsh 2009), but this needs more explicit investigation.

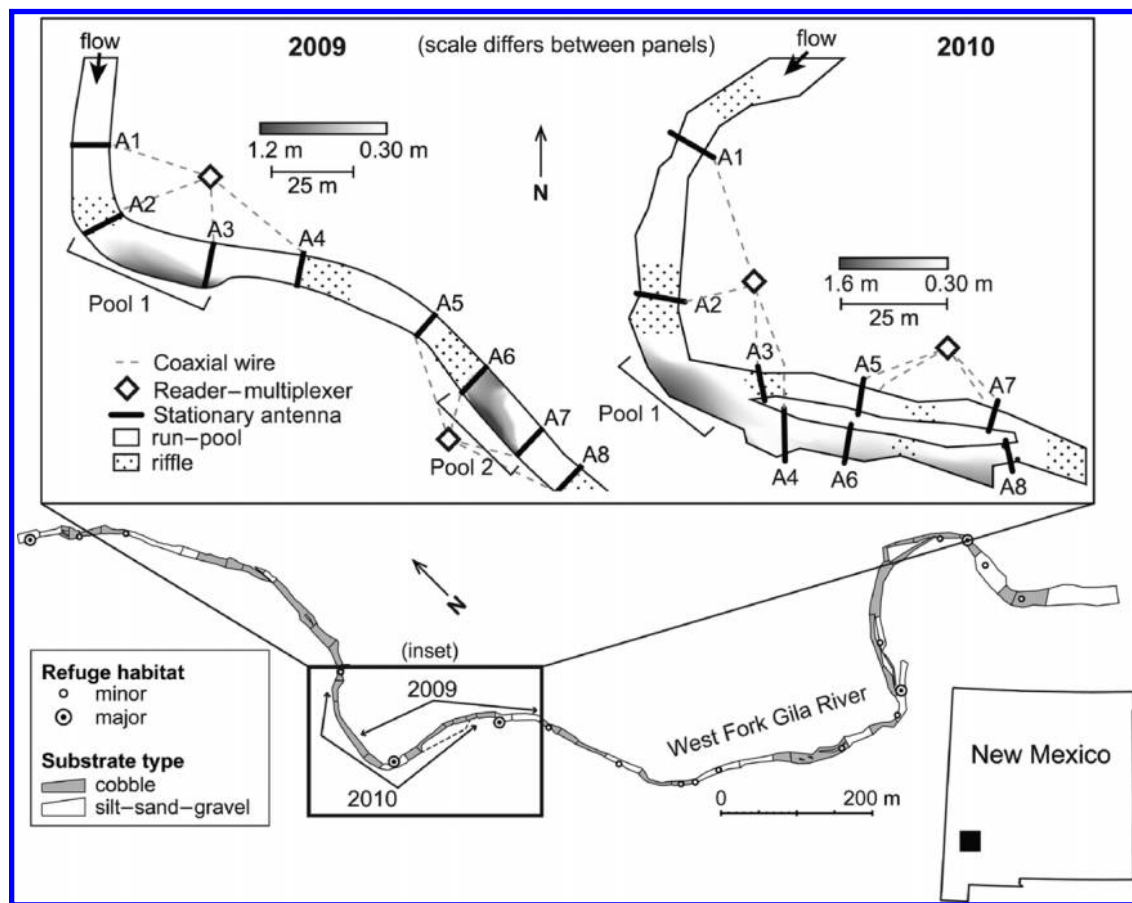
Study location

The upper Gila River is a tributary to the Colorado River that originates in the Mogollon Mountains of western New Mexico. Our study site at the Heartbar Wildlife area was located near the confluence of the West and Middle forks of the Gila River, approximately 3 km downstream from Gila Cliff Dwellings National Monument (Fig. 1). Flow in the Gila River is dominated by snowmelt, and the region also experiences a summer monsoon season (July–September), which can account for a substantial proportion of the total rainfall. To monitor discharge, a gauge rod was installed during the 2009 season, and water level was recorded at least once daily and more often if there was a flood event. During 2010, water level was recorded every 5 min using Hobo water level loggers (Onset Corp, Pocasset, Massachusetts) and a rating curve developed during the sampling period to estimate discharge (Gore 2007). As juveniles, both *C. insignis* and *C. clarkii* are abundant in the West Fork of the Gila, but as adults *C. insignis* dominates the fish community (ratio of *C. insignis* to *C. clarkii*: juveniles, 0.9:1; adults, 5.8:1; M. Booth, unpublished data).

Movement

We assessed movement patterns of suckers using PIT tags and a combination of a mobile antenna and stationary antenna arrays. Fish were captured for tagging using electroshocking, hoop nets, or fyke nets, and only fish greater than 180 mm standard length

Fig. 1. Map of stream substrate, consistently used refuge habitats, and location of focal stationary antenna reach. Refuge habitats were delineated based on size, frequency of fish occupancy, and the number of tagged fish detected (major habitat: $>3\text{ m}^2$, frequently occupied, >5 fish detected; minor habitat: $<3\text{ m}^2$, occasionally occupied, 1–4 fish detected). Note that the 2009 and 2010 reaches both contained pool 1, but the overall spatial extent of the 2009 reach was larger and incorporated an additional refuge habitat (pool 2). River morphology also changed between 2009 and 2010 (sharper bend at upstream end of reach and channel split below pool 1).



were tagged. Sampling efforts resulted in capture of large (i.e., taggable) individuals only in discrete refuge habitats (pools, root wads, undercut), which were mapped as described below. We implanted read-write half duplex PIT tags (134.2 kHz, 23 mm \times 3.85 mm, RI-TRP-WEHP, Texas Instruments, Dallas, Texas) 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). We tagged 431 *C. insignis* and 119 *C. clarkii* (Table 1) within a 1.8 km reach of the West Fork Gila River from 2008 to 2010 (May to July). Fish were weighed, measured, and released in the same location as they were captured. Because fish were only captured in discrete refuge habitats, capture–release GPS location was recorded as the center of the contiguous refuge habitat unit (habitats $< 20\text{ m}$ long). We mapped the tagging reach using a GPS each season, characterized habitat types, and created a GIS map to enable us to measure movement distances within the stream and estimate the area of different habitat types.

We used stationary and portable antennas to track the movement of the fish through our study reach. 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–datalogger (Oregon RFID, Portland, Oregon) and a custom fabricated aluminum waterproof antenna housing with a 2.5 m fiberglass pole. Tag information was displayed on a ruggedized palm computer (Meazure MEZ1000 Aceca International, New Zealand) connected via a Bluetooth wireless serial adaptor. We

recorded the habitat location and detection time for each tag. In general, fish were not present in shallow water during the daytime, and water clarity was sufficient to observe whether fish were present in water shallower than 50 cm, so we primarily searched with the portable antenna in deeper water ($>50\text{ cm}$) and all areas with overhead cover (e.g., roots, undercut banks), regardless of depth. If fish were observed in shallow water, scanning with the portable antenna was attempted by quietly approaching the fish from downstream of their position. Because fish that were not scanned by the reader could not be identified, no data was collected for individuals observed visually but not scanned ($N \approx 5$). Recapture (i.e., tag detection) location was recorded as the center of the refuge habitat unit.

From 18 May to 31 July 2009 and 2 June to 1 July 2010, we sampled a reach extending 1.3 km downstream and 1 km upstream of the 1.8 km tagging reach. In addition, we looked for fish outside of the full reach on two occasions (1 June – 3 June 2009 and 2010); 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 up to two times per season. We also 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. Surveys were completed within 5–8 h. Our definition of a home range was the area repeatedly traversed within a specific period of time (Hodder et al. 2007), also

Table 1. Size and number of Sonora (*Catostomus insignis*) and desert (*Catostomus clarkii*) suckers PIT-tagged in the 1.8 km study reach of West Fork of the Gila River and the number of fish tagged within the focal pools from 2008 to 2010.

Tagging year	<i>Catostomus insignis</i>			Pool 1		Pool 2		<i>Catostomus clarkii</i>		
	Standard length			N	N	Standard Length (mm)			N	N
	N	Mean ± SD	Range			N	Mean ± SD	Range		
2008	233	268 ± 79	(100–415)	65	25	73	186 ± 43	(104–370)	33	1
2009	174	259 ± 76	(145–464)	45	17	37	194 ± 37	(150–292)	16	1
2010	24	211 ± 49	(152–310)	0	10	9	210 ± 41	(153–294)	0	6
Total	431	261 ± 77	(100–464)	110	52	119	190 ± 41	(104–370)	49	8

described elsewhere as the “prevailing range” (Doncaster and Macdonald 1991), which may shift with season, life history, or environmental or demographic changes. Use of a short-term home range enables quantitative comparisons between behavior categories that may change, as described above. For each individual and year, we calculated home range as the maximum linear displacement between the two most distant detection locations within the individual fish's record (modified from Hodder et al. 2007). Only data from portable antenna detections were used to calculate home ranges.

PIT tags also were detected using stationary antennas that continuously monitored the passage of tagged fish past a fixed location in the stream. Stationary readers employed a data logger circuit board and multiplexer (OregonRFID, Portland, Oregon) and RF module, control board, and antenna tuner (RI-RFM-008B-00, RI-CTL-MB2B, RI-ACC-008B, Texas Instruments, Dallas, Texas). Readers and two sealed, 12 V deep cycle batteries (170 A-hours-battery⁻¹) were connected in parallel and secured in streamside plastic boxes. In 2009, batteries were replaced every 2–3 days, and in 2010 batteries were connected to 120 W solar panels with solar charge controllers. A ruggedized palm computer (Meazura MEZ1000 Aceeca International, New Zealand) was connected via a Bluetooth wireless serial adaptor to transfer data daily from the data logger and displayed individual tag identification, date, time of detection, and antenna ID. Antennas were constructed from a single loop of 8-gauge battery cable (BC8 R-250, Metra, Holly Hill, Florida), with the top leg supported by cable ties and nylon rope and the bottom leg buried in the stream bottom. Antennas ranged from 6 to 12 m wide and 0.5 to 1 m tall and were placed in the stream perpendicular to the flow; read range varied between 20 to 80 cm depending on tag orientation (highest range when tag perpendicular to antenna, lowest when parallel). Four antennas were attached to each of the two readers using twin-axial wire (20–40 m cable run from reader to antenna; Fig. 1), for a total of eight antennas, and the multiplexer cycled through all of the antennas approximately 2.3 times per second. In 2009, the antennas were placed at the breaks in a riffle–pool–riffle–run–pool–riffle section of stream (Fig. 1), allowing detection of animals entering or leaving the pool, moving into shallower water, or moving between pools. The pools (refuge sites) selected were centered within the tagging reach to maximize the number of tagged fish present and were representative of refuge habitat frequently used by suckers in the Gila River, characterized by typical depths of >1 m, overhead cover (e.g., woody debris or undercut banks), and depositional sediment. High flows during winter 2009 led to substantial changes in the stream morphology, and the stationary antenna site was relocated in 2010, bracketing a single pool and the adjacent shallow areas, to allow for better estimation of duration of use of shallow habitats (Fig. 1). We collected 65 days of data from the stationary antenna reach during 2009 and 28 days during 2010.

We tested PIT tag detection efficiency when antennas were installed and once during the middle of the sample period. Detection efficiency was assessed by passing a PIT tag enclosed in a neutrally buoyant container through the antenna field ten times

at evenly spaced intervals across the width of each antenna. Antennas were monitored daily and retuned during the sample period when current through the antenna dropped below 1.2 A or changed substantially (>0.2 A). Detection efficiency was calculated by the methods of Zydlewski et al. (2006).

Analyses

Stationary antennas continuously recorded any tag within the read range for the duration that it was present in the antenna field and quickly generated large data sets. For ease of analysis and to reduce database size, we merged detections of an individual in the same antenna that were less than 2 min apart. For analysis of turnover and residency, we divided the reach into segments (2009: upstream–A1; Pool 1 (A2–A4); Pool 2 (A5–A7); downstream–A8; 2010: upstream–A1; Pool 1 (A2–A4); shallow side channel (A5, A7); deep side channel (A6, A8)) and classified individuals based on the last antenna where they were detected during a 24 h period 1200–1200 (i.e., noon to noon; Fig. 1).

Although it is likely that a population exhibits a continuum of movement behaviors, for clarity of analysis we subjectively categorized individuals as “transient” (<10 days) or “frequent” (≥10 days) visitors to pool habitats. We chose these cutoff values based on a local minimum in a frequency analysis of the total visits each individual had to the pool habitats while limiting individuals classified as frequent to those that could be observed for at least ½ of the period when all antennas were installed. For frequent visitors to the two pools, we calculated the degree to which individuals exhibited preference or fidelity to one of the two pool habitats. We calculated fidelity as the proportion of observations in the most frequently visited pool divided by the total number of observations for the individual. Because the classification of individuals was independent of data used to generate home ranges, it was possible to compare home range size of frequent and transient visitors.

We calculated population turnover (T) as the number of fish that were classified as present in the focal pools as

$$(1) \quad T = 1 - \left(\frac{N_i \cap N_{i-d}}{N_i} \right)$$

where T is turnover, N_i is the tagged population detected in the pool on the current day, and the numerator is the number of individuals that are shared (intersection) between the current day i and d days prior to the current day. Daily turnover was calculated with $d = 1$ for Pool 1 (30 May to 26 July 2009, 1 June to 30 June 2010) and Pool 2 (27 June to 26 July 2009). Our expectation was that populations would be more similar between subsequent days, but the difference would increase over longer periods. To test for a correlation between turnover and time, we calculated turnover each day for $d = 1$ to $d = 24$ over the sampling period where all antennas were installed (27 June to 26 July 2009 and 1 June to 30 June 2010). Our definition for summer residency was that an

Table 2. Fish detected in the focal stationary antenna reach during 2009 and 2010 and the percentage of detected individuals that were tagged in that habitat.

Species	2009						2010		
	Upstream (Pool 1)		Downstream (Pool 2)		Both habitats		Total	Entire reach	
	N	% Tagged	N	% Tagged	N	% Tagged	N	N	% Tagged
<i>Catostomus insignis</i>	144	49	113	26	91	64	166	83	42
<i>Catostomus clarkii</i>	27	74	24	4	21	81	83	19	42

Note: The majority of *C. clarkii* tagged from 2008 to 2010 were captured in the upstream pool. In 2009, the focal reach included an upstream (Pool 1: antennas A1–A4) and downstream (Pool 2: A5–A8) refuge habitat. In 2010, the focal reach included one primary refuge habitat (Pool 1).

individual was detected for a minimum of 20 sampling days within the focal pool (2009: >25 days; 2010: >20 days).

Statistical analyses

We used ANOVA to test for differences in size between transient and frequent visitors to the study reach, with pool as a blocking factor. We used a Wilcoxon signed rank test to determine if frequent visitors exhibited strong fidelity to only one of the pools (hypothesized mean = 0.5, individual shows equal preference). For each year and species, we used ANOVA to compare the home range of frequent versus transient visitors. To assess whether population size was more variable between the pools, we used a χ^2 test for difference in standard deviation in population size. We used Wilcoxon signed rank to test for differences in the number of resident fish in pool 1 and pool 2 and used arcsine-square-root-transformed proportions in a *t* test to determine if the proportion of resident fish to the total population size was different between the pools. We used ANOVA to assess correlations between population size and turnover rate, as well as test for correlation between fish use of shallow habitats and stream discharge. For all tests, we considered $P \leq 0.05$ indicative of significance. All statistical analyses were completed using JMP 9 (SAS Institute, Cary, North Carolina).

Results

Detection efficiency was high in the central antennas for each pool in 2009 (>80%), but low in antennas 4 and 5 (<30%) because of lower amperage from longer cable runs (40 versus 20–25 m; Fig. 1). Because of their location in the array, missed detections on antennas 4 and 5 do not influence estimates of residency or turnover, but may have influenced our classification of behavior type. In 2010, detection efficiency was typically high (>80%), except for antenna 3 (50%). Antennas were functional throughout the study period, except for a single failure during a spate on 25 June 2009, when several antennas were displaced by flood-borne debris. Antennas were repaired and replaced within 3 h of the spate.

Of the 550 *C. insignis* and *C. clarkii* tagged between 2008 and 2010 in the 2 km reach of the West Fork Gila River, we detected 249 fish in 2009 and 102 fish in 2010 in the 200–300 m stationary antenna reaches (Table 2). Because it was not logistically possible to perform depletion electroshocking, our estimates of the proportion of fish tagged are based on limited data (two sampling events) from passive capture in hoop nets. Based on the proportion of tagged fish captured in hoop nets during 2009, we estimate that 45%–80% of the fish present in the focal reach contained PIT tags. Nearly half of fish detected within pool 1 in both 2009 and 2010 were individuals that were tagged in pool 1, and the majority of individuals observed in the upstream and downstream reaches were tagged within pools 1 and 2, indicating that some individuals tagged in this section of stream exhibited fidelity to these pool habitats. We observed nine individuals that were frequent (≥ 10 times) visitors in both 2009 and 2010 and 31 individuals that were observed at least once in both years.

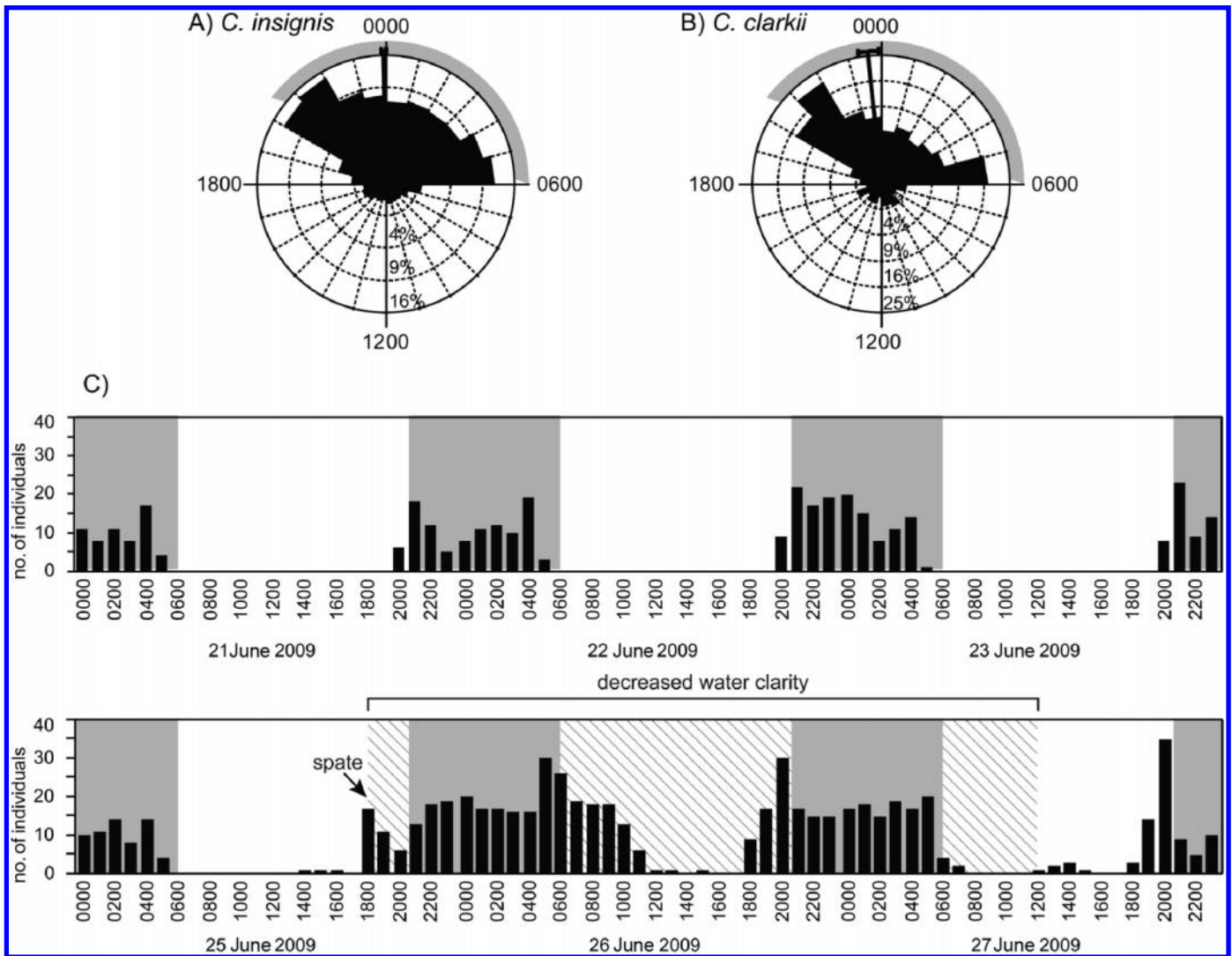
Fish typically moved through antennas and into shallow water (<50 cm) to feed during the night, with crepuscular peaks in activity (Figs. 2A–2B). Some individuals made occasional forays through the antenna array during daylight hours, but visual observations confirmed that most fish were concentrated in pool habitats and under overhead cover. Occasionally, one to five fish were observed foraging in refuge habitats during the day.

Individual *C. insignis* exhibited intrinsically different movement patterns as well as different responses to environmental changes like spates (Fig. 3). However, there were several general behavior categories observed in each year. In 2009, the major behavior categories were (1) occasional forays (typically observed in only one antenna, with occasional longer movements), (2) regular forays (consistent movement through multiple antennas), and (3) transient-directed (movement through the entire reach, with only brief visitations to the focal reach). In 2010, we observed similar behaviors, but additionally observed individuals that only used the side channel portion of the reach (Table 3). We had sufficient data for 97 individuals to determine their response to the spate in 2009. Fish exhibited several responses — individuals made a brief (<3 day) displacement out of the reach (e.g., Fig. 3A; 29 individuals), sustained displacement to an alternative habitat (e.g., Fig. 3D; upstream: 32 individuals, downstream: 12 individuals), or showed no change in their activity (e.g., Figs. 3C and 3E; 24 individuals).

Approximately half of the *C. insignis* and *C. clarkii* were transient visitors to the stationary antenna reach during 2009, but the majority of *C. insignis* were transient visitors in 2010 (Fig. 4A). Transient fish (mean \pm SD: 271 \pm 11 mm) were similar in standard length to frequent visitors (287 \pm 7 mm, $F_{[2,130]} = 2.203$, $p = 0.11$). Most frequent visitors to the reach in 2009 exhibited strong fidelity to only one of the pools (hypothesized mean = 0.5, Wilcoxon signed rank, $p < 0.0001$; Fig. 4B), although eight *C. insignis* and two *C. clarkii* used both pools in a similar proportion. In pool 1, 39 of the 52 frequent visitors were originally tagged in pool 1, while in pool 2, 24 of the 54 frequent visitors were tagged in pool 2. Frequent visitors typically had significantly smaller home ranges than transient visitors (mean \pm SE; *C. insignis* 2009: frequent (374 \pm 56 m), transient (795 \pm 82 m), $F_{[1,131]} = 17.97$, $p < 0.0001$; 2010: frequent (93 \pm 166 m), transient (481 \pm 97 m), $F_{[1,42]} = 4.0743$, $p = 0.05$; *C. clarkii* 2009: frequent (168 \pm 134 m), transient (819 \pm 156 m), $F_{[1,24]} = 9.473$, $p = 0.005$; 2010: frequent (110 \pm 233 m), transient (603 \pm 165 m) $F_{[1,7]} = 2.966$, $p = 0.13$). However, half of the frequent and transient *C. insignis* showed home ranges <250 m.

Population size (the number of tagged fish detected within a 24 h period 1200–1200) of *C. insignis* was more variable in pool 1 than in pool 2 during 2009 (pool 1 mean \pm SD: 31 \pm 10 individuals, pool 2: 33 \pm 6 individuals; $\chi^2 = 14.06$, $p = 0.002$; Fig. 5). The number of resident fish (individuals spending >25 days within the habitat) was lower in pool 1 than in pool 2 (Fig. 5; Wilcoxon signed rank, $p < 0.0001$) and typically made up a larger proportion of the total daily population in pool 2 (pool 1: 27%, pool 2: 46%; *t* test arcsine-square-root-transformed, $t = 18.335$, $df = 30$, $p < 0.0001$). Daily

Fig. 2. Timing of movement through stationary antennas for (A) *C. insignis* and (B) *C. clarkii* based on all detections from 2009 and 2010. Thick, solid black line indicates overall mean and SE of movement timing, the grey semicircle indicates night, and values represent the percentage of observations during each time period. (C) Timing of daily movements through stationary antennas before (upper panel) and during a period of decreased water clarity (cross-hatching, lower panel) following a spate in 2009. Visibility was 0 m directly following the spate gradually increasing to >0.5 m. Both *C. insignis* and *C. clarkii* showed a similar response, and because only three *C. clarkii* were observed during this period, all data are combined for clarity. Data are from all antennas in the focal reach.



turnover was variable in both 2009 and 2010, ranging from 0% to >60%. There was no relationship between the change in population size between days and the turnover rate ($r^2 < 0.001$) for either pool in 2009, but in 2010 turnover was positively correlated with the change in population size ($F_{[1,29]} = 9.887$, $p = 0.004$). In 2009, high turnover in pool 2 was partially driven by individuals moving from pool 1 into pool 2 ($F_{[1,28]} = 16.23$, $p = 0.0004$), but high turnover in pool 1 was not related to individuals moving from pool 2 into pool 1 ($F_{[1,28]} = 2.699$, $p = 0.112$). The individuals composing the population were more similar over short time scales (1–2 days) than long time scales (weeks) (Fig. 6; $F_{[3,1328]} = 213.893$, $p < 0.0001$). Turnover rates were higher in 2010 than in 2009.

In addition to the individual behavioral responses to the spate in 2009, hydrology influenced movement behaviors in both years of study. The brief spate substantially decreased water clarity from 25 June 2009 at 1605 (zero visibility) until 27 June 2009 at 1400 (0.5 m visibility), and fish activity continued into daylight hours (Fig. 2C). In 2010, fish use of the shallow side channel habitats (A3, A5, A7) was related to discharge (Fig. 7). As discharge and water depth decreased, substantially fewer individuals used the

side channel ($F_{[1,59]} = 31.891$, $p < 0.0001$) when the average side channel depth was <10 cm. We observed a greater drop in detections in A5 and A3, indicating that those that used the channel did not travel as far upstream. The number of individuals using each antenna in the main reach as a whole did not change over time, except for a slight reduction in antenna 1 as discharge decreased (ANOVA $F_{[1,30]} = 4.913$, $p = 0.034$).

Discussion

The findings of this study clearly demonstrate the importance of small-scale movement and population turnover in structuring stream fish assemblages. We observed that both *C. insignis* and *C. clarkii* made regular forays into shallow habitats during the evening, and movement into and among habitats was influenced by changes in flow (e.g., spates and low discharge). High rates of movement resulted in changes to population-level parameters including fluctuations in population size and turnover of individuals within a habitat over the course of the study. Although many individuals made frequent forays outside of the refuge sites, some

Fig. 3. Movement behaviors for individual *C. insignis* during the 2009 and 2009 study season, highlighting major behavior categories. Dashed lines delineate the upstream antenna reach from the downstream reach (A–E) or the side channel antennas (F–J). *Catostomus clarkii* displayed movement behaviors that fit within these categories. Major behavior categories: (A, E, I) limited forays (typically observed in only one antenna, with occasional longer movements), (B) transient–directed (movement through the entire reach, with only brief visitations to the focal reach), (C, D, F, G, H, J) regular forays (consistent movement through multiple antennas). Some individuals made frequent forays into the shallow side channel in 2010 (e.g., H). Flood responses are shown in panels A, C, D, E. Date format for x axis is month/day.

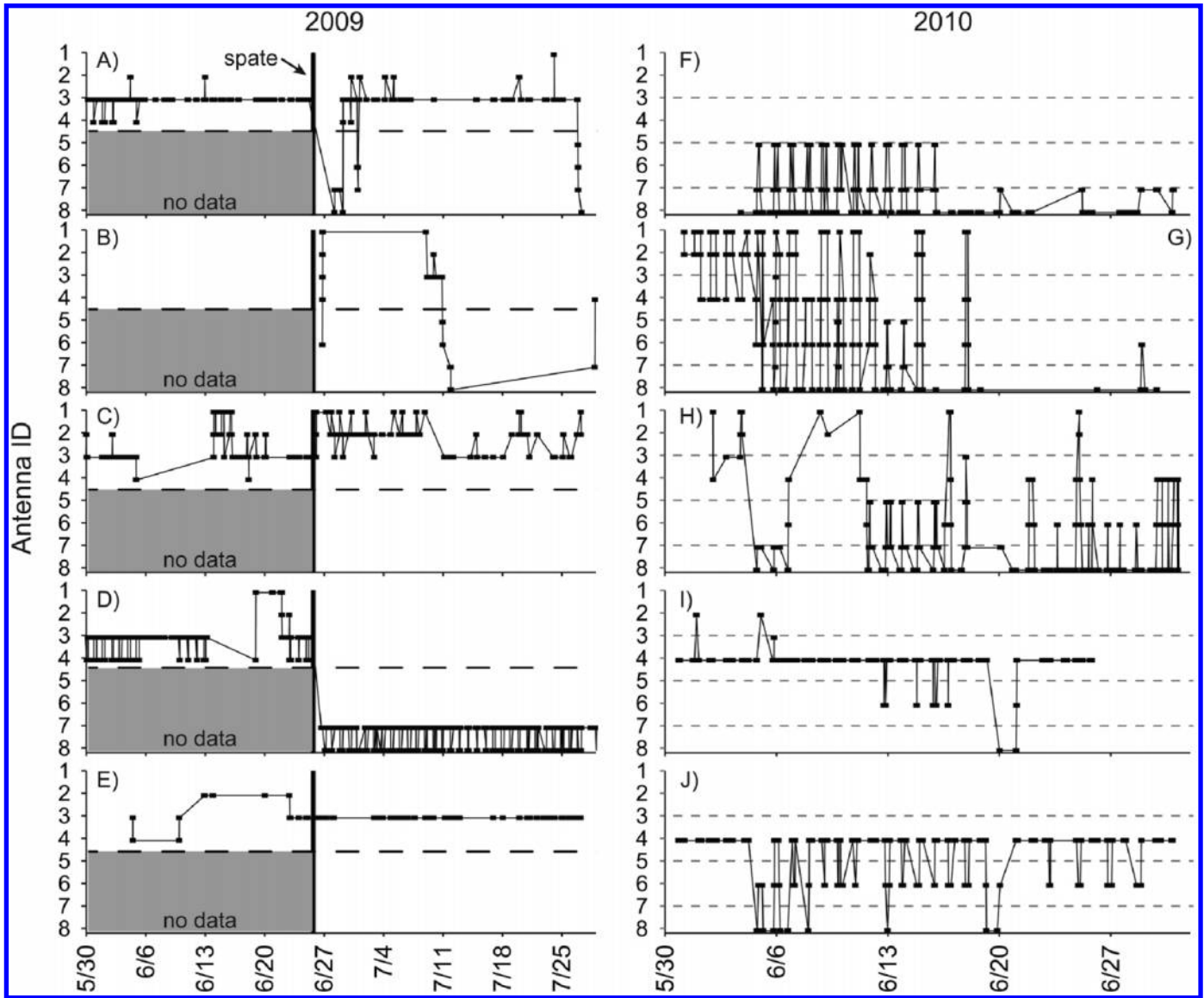


Table 3. Individual movement patterns for Sonora and desert suckers, based on their entire movement record for each study year.

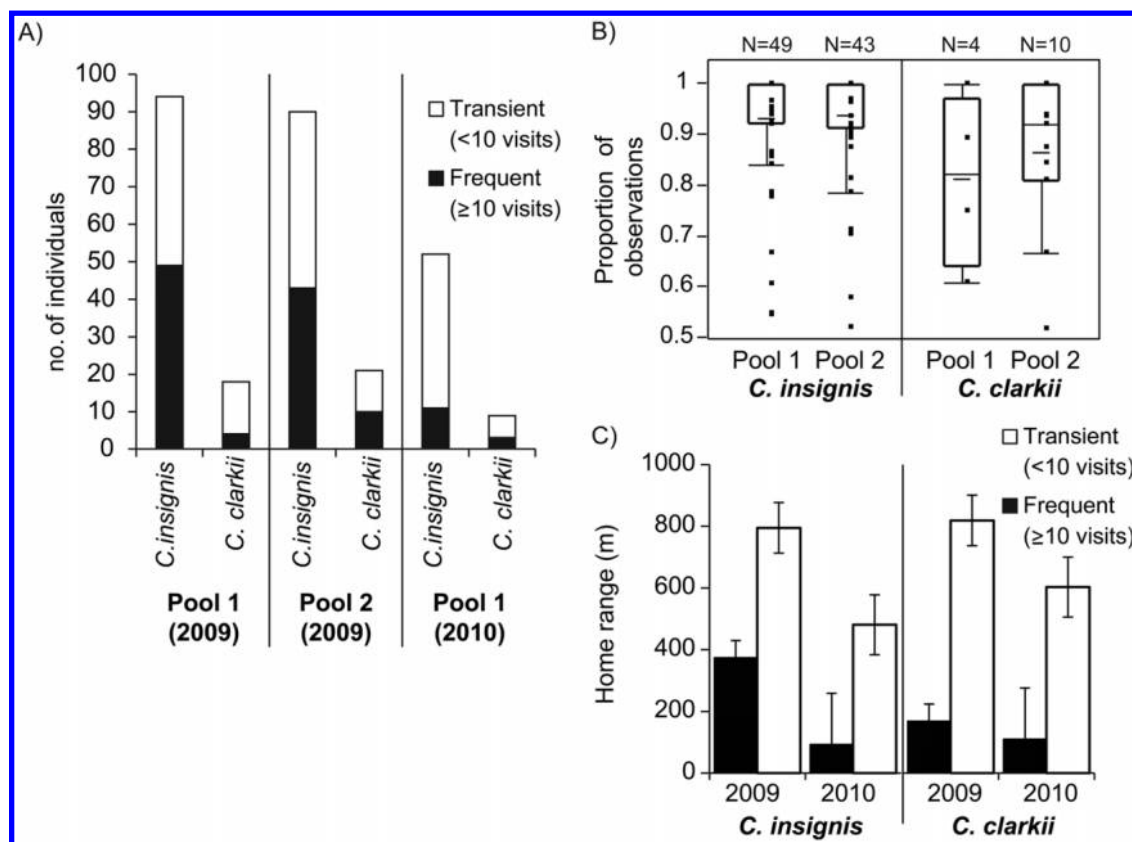
Year	<i>Catostomus insignis</i>				<i>Catostomus clarkii</i>			
	Limited	Regular (side channel)	Transient–directed	Other	Limited	Regular	Transient–directed	Other
2009	15	82	68	1	2	13	14	1
2010	4	30 (3)	46	0	0	3	16	0

Note: Fish were classified as “limited” (primarily detected in a single antenna with rare excursions into other antennas), “regular” (regularly moved through at least two antennas), “transient–directed” (brief incursions into the study reach, often with consistent upstream or downstream trajectory), or “other”. In 2010, some individuals only used the shallow side channel of the focal reach (antennas A5, A7).

individuals displayed remarkable fidelity to a single focal refuge during a summer season and occasionally between years. Our results indicate that population turnover was quite high (Figs. 5 and 6) for sucker populations in the Gila River and that the com-

bination of site fidelity with frequent, small-scale movement may provide a partial explanation for the observation in other systems that many adult fish appear to be sedentary (Gerking 1959). Fish activity was concentrated during the night, with occasional forays

Fig. 4. (A) Proportion of *C. insignis* and *C. clarkii* detected within each habitat and season that were frequent (≥ 10 visits) or transient (< 10 visits) visitors to habitats within the focal reach. (B) Fidelity of frequent visitors to one habitat within the focal reach in 2009. Fidelity was calculated as the proportion of total visits where the individual was detected within the more frequently visited habitat. Fidelity of 0.5 indicates equal use of both pools. Each point represents an individual fish. The ends of the box are the 25th and 75th quartiles, the line across the middle of the box is the median sample value, and whiskers are $\pm 1.5 \times$ interquartile range. (C) Mean \pm standard error home range for transient and frequent fish.



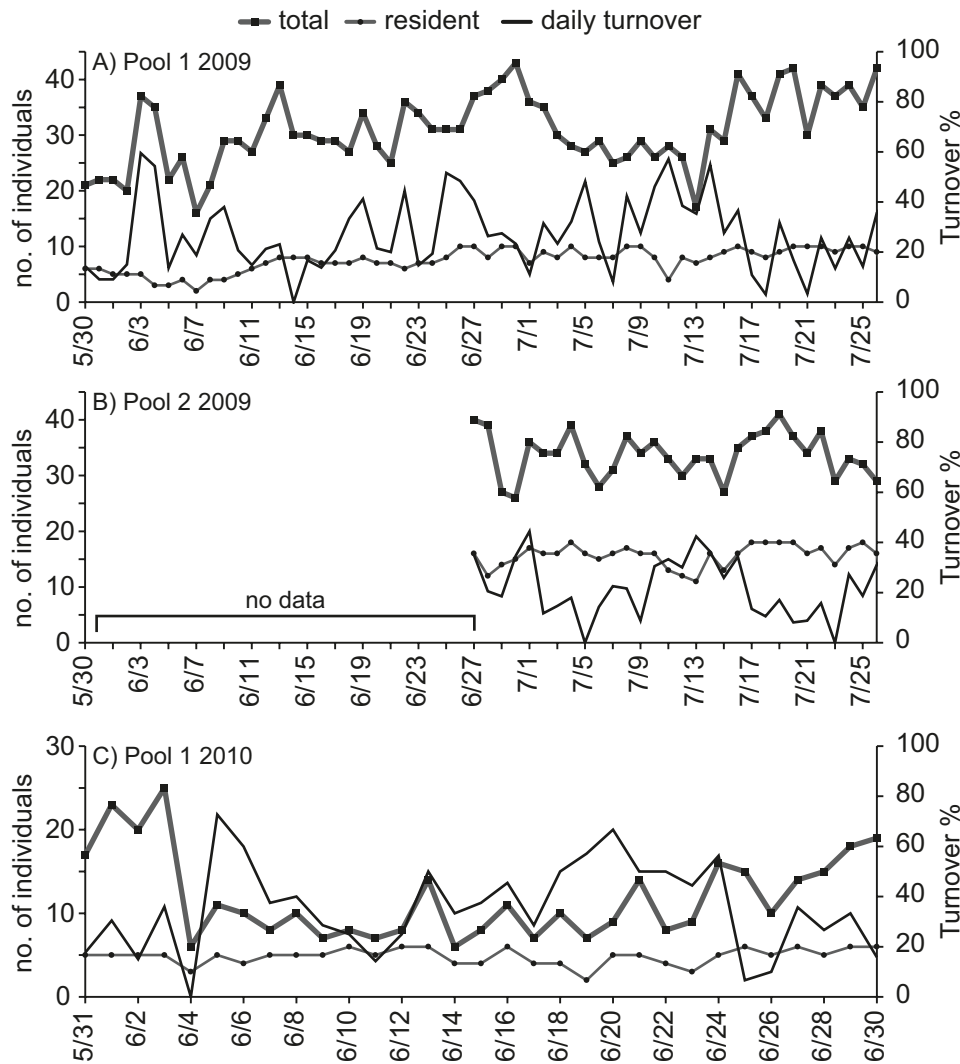
into shallow water during the day (Fig. 2). All of the daytime refuges occupied by fish provided substantial overhead cover, and movement patterns coincided with incident light. In addition, fish activity responded quickly to changes in water clarity, with activity extending into daylight hours while water was turbid during a spate. Nocturnal behavior and response to water clarity suggests avoidance of visual predators, whose ability to capture prey is directly related to light availability and turbidity (Aksnes and Giske 1993). Although we did not observe direct predation on large fish, the presence of piscivorous birds in the area (e.g., mergansers, herons, osprey) and beak-shaped scars on fish indicate that predation risk may explain avoidance of shallow habitats during the daylight hours.

Because adult fish primarily remain in refuge sites during the day, spatial knowledge of the overall stream landscape may be of crucial importance for an individual (Bernstein et al. 1991; Gowan and Fausch 2002) if this enables it to make nighttime foraging forays into high resource habitats to forage and then return to refuge sites. Stream salmonids appear to monitor habitat conditions at a reach scale (hundreds of metres), and when large, competitively dominant individuals are denied access to their preferred feeding habitat, many move to a new habitat rather than displace subordinate individuals within their habitat (Gowan and Fausch 2002). Because of differences in foraging behavior between salmonids and suckers, we do not expect displacement to result from interference competition between suckers (Baltz and Moyle 1984), but it seems likely that individuals may monitor conditions at the reach scale for other reasons. Indeed, we observed that individuals make similar foraging movements

from day to day (e.g., Figs. 3D, 3F, 3J), suggesting that fish may be familiar with a particular section but occasionally investigate other sections of the stream while foraging. The home range-shift conceptual model of Crook (2004) suggests that sometimes these forays into other habitats may result in a permanent or extended shift of the home range to a new location. Other species of fish, including other suckers, show similar diel movements between distinct habitats (Matheny and Rabeni 1995; Arrington and Winemiller 2003), suggesting that frequent forays out into adjacent habitats may be a common theme in stream fishes, although the extent of these movements likely varies among taxa. Foraging theory suggests that individuals should seek new habitat when the fitness increase experienced by moving outweighs the fitness realized by remaining in their current habitat (Charnov 1976; Gowan and Fausch 2002). Assessing the environment is advantageous when the quality of the environment varies spatially and temporally, even if habitat assessment is costly (Richards and De Roos 2001). If the consumer's movement is large compared with the spatial distribution of resources, consumers that move will have more complete knowledge of resource availability and thus be able to make more ideal decisions for habitat switching (Bernstein et al. 1991).

Sucker movement, however, must account for access to food resources as well as availability of daytime refuges. Both species are capable of substantial movements within short periods ($> 1 \text{ km} \cdot \text{day}^{-1}$; M. Booth, unpublished data) and thus can access high-quality habitats distant from refuges, but potentially risk predation if they are unable to locate a daytime refuge. The preference for a particular pool we observed for frequent-visitor fish

Fig. 5. Daily turnover (see Methods), number of resident fish (observed ≥ 25 times), and total number of *C. insignis* last observed within (A) Pool 1 in 2009, (B) Pool 2 in 2009, and (C) Pool 1 in 2010. No data available for Pool 2 in June 2009 because antennas were not yet installed. Date format for x axis is month/day.



may be due to knowledge about the availability of refuge sites in the focal reach, although other explanations (e.g., minimizing energy expenditures) cannot be discounted. Other fishes (e.g., suckers, carp, catfish) appear to have home habitats from which they make regular forays (Matheny and Rabeni 1995; Crook 2004; Vokoun and Rabeni 2006), and it is possible that this behavior is common in other taxa as well. Vokoun and Rabeni (2006) suggest that some taxa, like flathead catfish (*Pylodictis olivaris*), may be less sedentary than previously thought because they move at time scales shorter than most studies can detect and show fidelity to particular locations in the stream. Similarly, Sonora and desert suckers appear to be more mobile than previously described (Bestgen et al. 1987).

High turnover of individuals (fish leaving the marking reach) has been offered as an explanation for the observation that many fish marked in mark-recapture studies often are never recaptured (Rodríguez 2002). Although stream salmonids commonly show high turnover but short movement distances (Hilderbrand and Kershner 2000; Rodríguez 2002; Schrank and Rahel 2006), there is disagreement whether there is a consistent relationship between turnover and displacement (Gowan et al. 1994; Rodríguez 2002). Our findings suggest that individuals transiently visiting a section of stream tend to have larger home ranges than individuals fre-

quently observed in that habitat. However, about half of the transient individuals showed small home ranges (<250 m) and half of the frequent visitors made forays to distant habitats, resulting in large home ranges (500–1500 m). A large proportion of the population in the focal pools were transient visitors, often from locations up to several kilometres away, and individuals who frequently visited the pools also made extended forays outside of the focal antenna reach, contributing to daily population turnover. High turnover potentially provides some explanation for fish that are not recovered in mark-recapture studies (i.e., many fish move, potentially limiting recapture), but high turnover in our study resulted in a wide range of displacement distances.

Ranging behavior (short-term exploratory behavior) has been documented in salmonids (Gowan and Fausch 2002; Schmetterling and Adams 2004; Schrank and Rahel 2006) as well as other taxa (Crook 2004; Hodder et al. 2007) and is thought to be related to changing environmental conditions and resource availability (Gowan and Fausch 2002). However, displacement distances are typically limited. Salmonids typically feed on drifting invertebrates that are replenished from upstream sources and so individuals compete for relatively small feeding stations to access resources in the drift (Fausch and White 1981; Baltz and Moyle 1984). Unlike the drift, resources in patches of benthic habitat

Fig. 6. Population turnover for *C. insignis* over time, ranging from 1 to 24 days. Data points are mean \pm standard error of turnover rates (see Methods) for (A) Pool 1 in 2009, (B) Pool 2 in 2009, and (C) Pool 1 in 2010.

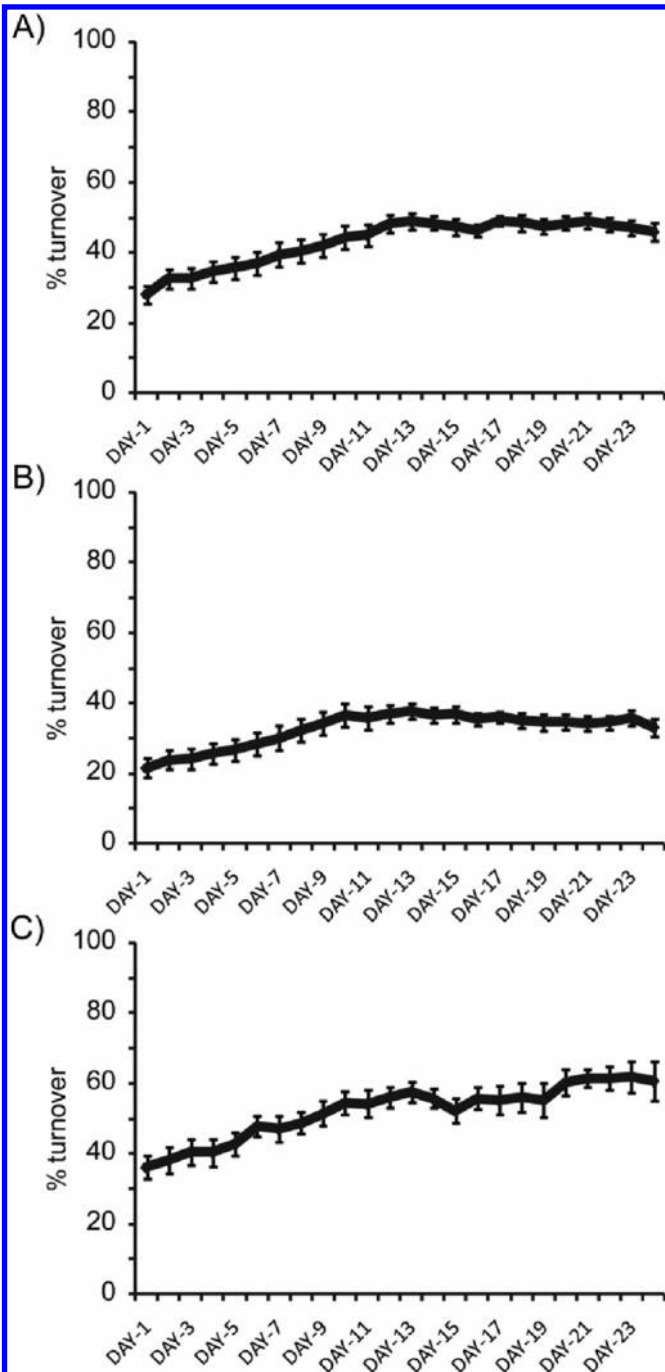
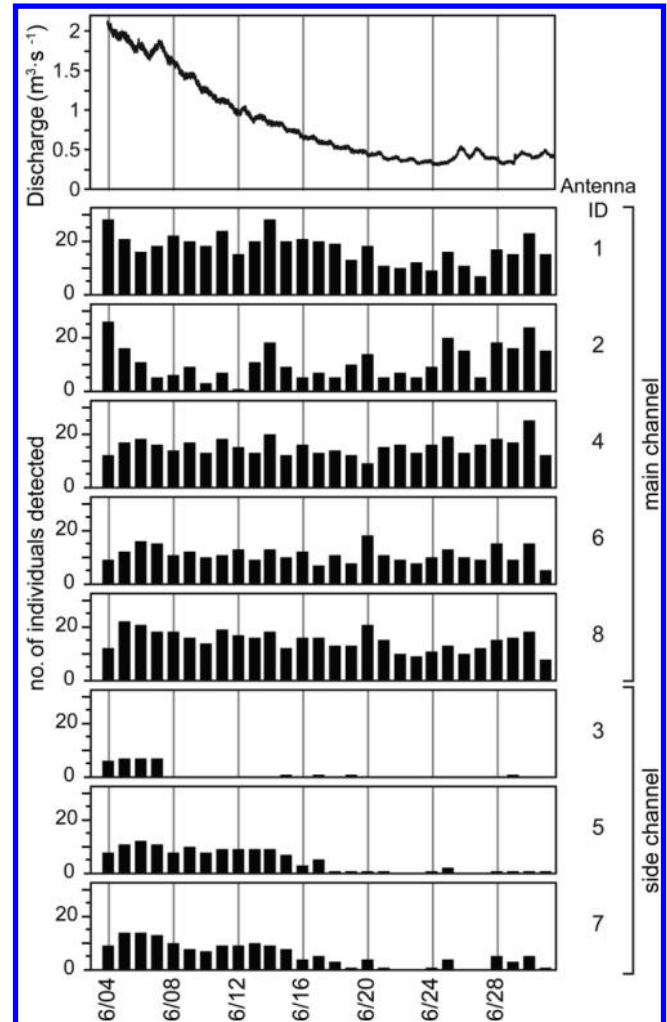


Fig. 7. Fish use of main channel and shallow side channel habitat in relation to stream discharge. Average depth in antennas A5 and A7 was <10 cm at minimum discharge. Date format for x axis is month/day.



not related to distance to refuge habitats. M. Booth (unpublished data) also observed that *C. insignis* may use lower quality refuge habitats occasionally during low water but regularly during high water periods. Extended foraging trips into habitats distant from refuge sites may temporarily strand fish away from their preferred habitats, causing them to utilize the closest available refuge site instead of returning to a home pool. Short-term displacements, whether intentional or accidental, potentially explain high daily turnover rates.

Although a small number of resident fish was consistently found within the focal pools, the overall population within the focal reach fluctuated over time as fish moved among habitats. Variation in population size over time may be problematic for assessing habitat quality based on population density, while movement parameters (e.g., immigration and loss) can be used to create metrics that provide more stable estimates of habitat quality (Bélanger and Rodriguez 2002). Some population fluctuations appeared to be related to increased movement during spates as well as electrofishing within the study reach (M. Booth, unpublished data), but many others had no apparent explanation. Small-scale and short-term movements may keep populations relatively fluid and distribute resource consumption over the stream as a whole (M. Booth, unpublished data). In addition, fish quickly began moving in response to spates, giving fish rapid access to newly

inundated habitat with potentially novel resources. Turnover increased over time, leading to populations within the pools that substantially differed in the individuals present between the beginning and end of the monitoring period. Constant reshuffling of individuals within populations and consistent small-scale movements may allow fishes to recolonize habitats after disturbances and could serve to maintain genetic exchange within streams as a whole.

Stream hydrology, at both high and low flows, influenced sucker movement behavior. As expected, low flows eventually limited movement into shallow habitats (Fig. 7) and in particularly dry years could prevent movement between refuge habitats altogether. Movements into shallow habitats became more rare as the stream approached the critical depth threshold. Reduced movement at low water levels can potentially have major consequences, increasing immigration and crowding in refuge habitats (Magoulick and Kobza 2003) and creating fundamental shifts in species dynamics (Power et al. 1985).

At the other end of the flow spectrum, movement responses to spates varied widely within the population, with individuals showing no response, temporary displacement to another location and subsequently returning to their home pool, or sustained displacement to an alternative habitat. Within-species variation in response to high flow events has been observed in other species of suckers (Jeffres et al. 2006) as well as in galaxiids (David and Closs 2002), while some fish show no response to high flow events (e.g., hitch (*Lavinia exilicauda*); Jeffres et al. 2006). The way native species respond to floods is of particular importance in the western USA, where controlled flood events have been used as management tools (Valdez et al. 2001; Jeffres et al. 2006) to reduce non-native species, assuming that native taxa are better adapted to resisting flood events (Meffe 1984; Schultz et al. 2003). Particularly in flood-prone or flow-regulated streams, accounting for variation in flow responses within and among species will be critical for managing fish populations.

Diel and small-scale movements can influence local population size and composition of individuals and species within habitats. Site fidelity and diel movements may potentially explain why large proportions of populations may appear sedentary (Rodríguez 2002) and indicate that the frequency of sampling efforts may change estimates of home ranges for many stream fishes. Knowledge of variation in movement patterns among species and habitats as well as over long time frames will increase our ability to properly design conservation strategies and manage local fisheries.

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