Journal of Freshwater Ecology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tjfe20

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Published online: 03 Oct 2012.

To cite this article: Maria C. Dzul , Michael C. Quist , Stephen J. Dinsmore , D. Bailey Gaines & Michael R. Bower (2013) Coarse-scale movement patterns of a small-bodied fish inhabiting a desert stream, Journal of Freshwater Ecology, 28:1, 27-38, DOI: 10.1080/02705060.2012.718250

To link to this article: http://dx.doi.org/10.1080/02705060.2012.718250

Journal of Freshwater Ecology, 2013
Vol. 28, No. 1, 27–38, http://dx.doi.org/10.1080/02705060.2012.718250

Coarse-scale movement patterns of a small-bodied fish inhabiting a desert stream

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(*Received 26 April 2012; final version received 8 July 2012*)

Located on the floor of Death Valley (CA, USA), Salt Creek harbors a single fish species, the Salt Creek pupfish, *Cyprinodon salinus salinus*, which has adapted to this extremely harsh environment. Salt Creek is fed by an underground spring and is comprised of numerous pools, runs, and marshes that exhibit substantial variability in temperature, salinity, and dissolved oxygen concentrations. In addition, the wetted area of Salt Creek is reduced throughout the summer months due to high rates of evaporation, with some reaches drying completely. Therefore, it seems logical that short- and long-term movement patterns may play an important role in Salt Creek pupfish population dynamics. The objective of this study was to describe coarse-scale movements of Salt Creek pupfish in Salt Creek during their breeding season from March to May. Sex ratios and length–frequency distributions varied spatially within Salt Creek, suggesting population segregation during the breeding season. Long-distance movements were generally rare, although two fish moved more than 1.2 km. Movement in upstream reaches was rare or absent, in contrast to the greater movement observed in downstream reaches (29% of recaptures). Temporal trends and demographic patterns in movement were not observed. Because the two most downstream habitats dry up in the summer, our results indicate that coarse-scale movements that re-populate downstream reaches likely occur during other times of year. Consequently, the importance of small- and large-scale movements is influenced by season. Further assessment of Salt Creek movement patterns conducted during other times of year may better illuminate long-distance movement patterns and source-sink dynamics.

Keywords: movement patterns; sex ratio; pupfish; Death Valley; desert streams

Introduction

Mechanisms that instigate movement by fishes are often difficult to generalize because movement patterns are influenced both by species life history characteristics

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and spatio-temporal variation in environmental conditions. Specifically, potential benefits (e.g., improved abiotic conditions and reduced competition) of movement are countered by risks or barriers to movement (e.g., predation and habitat connectivity), both of which vary by species and life history state (Albanese et al. 2004; Davey and Kelly 2007; Roberts and Angermeier 2007). Studies that estimate movement can help determine the importance of connectivity in aquatic systems (Johnston 2000; Fausch et al. 2009) as well as increase understanding of species' life history (e.g., Goforth and Foltz 1998; Roberts and Angermeier 2007). For example, because harsh environmental conditions in desert stream environments could be partly offset by habitat complexity and diversity of refugia, studies evaluating movement may help biologists determine the role of refugia in population persistence (Labbe and Fausch 2000; Magoulick and Kobza 2003). Importantly, mechanisms influencing movement may differ for individuals and populations (Dingle and Drake 2007). Non-random spatial and temporal patterns in movement suggest population-level responses to environmental factors, whereas random movement might be attributed to factors influencing individuals. As such, our use of the word 'movement' will refer to fish displacement between habitats with different environmental characteristics, whereas 'dispersal' will refer to temporally or spatially organized unidirectional movement of a group of individuals between habitats.

This study describes movement patterns of Salt Creek pupfish, *Cyprinodon salinus salinus,* inhabiting Salt Creek in Death Valley National Park, CA, USA. Salt Creek is a temporally dynamic and spatially complex environment for its sole aquatic vertebrate resident, the endemic Salt Creek pupfish. Previous studies have documented short-distance movement of pupfishes between habitats of varying depth in response to thermal conditions (Barlow 1958; James 1969; Sada and Deacon 1995) but to our knowledge, movement patterns of pupfishes over coarse habitat scales remain unexplored. Accordingly, this study was initiated to determine whether Salt Creek pupfish disperse during their spring breeding season.

We hypothesized that spatial, temporal, and demographic factors may influence movement patterns. Specifically, because limited resource availability often promotes emigration (McMahon and Tash 1988; McMahon and Matter 2006), we hypothesized that the upstream perennial regions are a source habitat that supplies individuals to downstream ephemeral sink habitats. Additionally, we hypothesized that movement rates will decrease throughout the course of the study, as pupfish establish breeding territories. Lastly, based on the results of McMahon and Tash (1988), we hypothesized that fish that move will be preferentially comprised of small males relative to fish that remain sedentary. Small males might be the most mobile demographic group if they are frequently displaced from high-quality breeding habitat by larger males. An understanding of Salt Creek pupfish movement patterns will help in the assessment of the importance of habitat connectivity in Salt Creek, while also providing insight into relationships between Salt Creek pupfish and their environment.

Methods

Study organism

Numerous physiological studies of pupfishes *Cyprinodon* spp. in laboratory environments indicate that pupfishes can tolerate temperatures up to 42°C

(Brown and Feldmeth 1971) and salinities up to 88‰ (Naiman et al. 1976). Although pupfishes can tolerate high temperature and salinity conditions, they will avoid harsh conditions by moving into more benign microhabitats when in their natural environment (Barlow 1958). In addition, pupfishes can tolerate temperatures near freezing (Brown and Feldmeth 1971; Feldmeth et al. 1974). The ability to acclimate to a wide temperature range is an important adaptation for organisms inhabiting desert stream environments because environmental conditions in desert streams undergo large daily and seasonal fluctuations. Peaks in Salt Creek pupfish spawning occur in spring and early autumn (Sada and Deacon 1995) and mortality is greatest in summer due to extreme temperatures and loss of wetted habitat (Miller 1943; Sada and Deacon 1995). Although the mean lifespan of pupfishes is thought to be one year (Kodric-Brown 1977; Soltz and Naiman 1978), age and growth studies suggest that the mean lifespan of some pupfish species may exceed one year (Jester and Suminski 1982). Williams and Bolster (1989) observed increased Salt Creek pupfish mortality following a flash flood. Specifically, peripheral habitats created by the flood event later became isolated from the mainstem and eventually evaporated completely, thus killing all fish that had become stranded in isolated pools.

Study site

Salt Creek, located in Death Valley, is perhaps one of the most extreme desert stream environments home to vertebrate taxa. Specifically, Salt Creek is composed of numerous pools, runs, and marshes that experience large seasonal fluctuations in temperature, salinity, and wetted area (Sada and Deacon 1995). The source of water for Salt Creek comes from McLean Spring, a groundwater spring. Although temperature conditions in some reaches of Salt Creek vary from near freezing to 40°C and experience varying salinity concentrations up to that of seawater (Moyle 2002), environmental conditions in deeper reaches of Salt Creek remain more stable. Similarly, annual variation in temperature, salinity, and habitat size is low near the source, and increases downstream (Sada and Deacon 1995).

We identified four different habitat types located along a longitudinal gradient in Salt Creek (listed from upstream to downstream): headwater, wetland, confined, and braided regions. Habitats were unequal in length and delineated by fish biologists based upon environmental characteristics. McLean Spring supplies water to Salt Creek at the headwater region. The headwater region (62 m in length) consisted of two deep pools with fine substrate and moderate aquatic vegetation. The wetland region (702 m in length) was comprised of numerous large, shallow pools with fine substrate and abundant aquatic vegetation. Pools in the wetland region were often separated by densely vegetated marshes that had potential to hinder movement between adjacent pools. The confined region (246 m in length) was a heterogeneous mixture of microhabitats ranging from relatively stagnant pools to shallow runs. In general, microhabitats in the confined region that were stagnant pools often had fine substrate bottoms with little to no aquatic vegetation, whereas shallow runs had no aquatic vegetation and hardened substrate. The braided region (236 m in length) was shallow, devoid of vegetation, and had sandy substrate. Whereas the headwater region has perennial stream flow, the confined and braided regions become intermittent and typically desiccate completely during summer (Sada and Deacon 1995).

Similarly, wetted area of the wetland region decreases during summer months. Spawning behavior was noted in shallow habitats located throughout Salt Creek. Gravid females were commonly found in all habitats, suggesting that spawning was likely occurring throughout all regions of Salt Creek. We intentionally incorporated large areas (referred to as 'buffer' zones) separating habitats to distinguish large- and small-scale movements.

Sampling methods

Sampling occurred from 1 March to 18 May 2010 and included three marking events and nine recapture periods. Marking events were spaced four weeks apart and lasted eight days, and recapture periods occurred weekly following each marking event. Recapture events lasted two to three days. Sites located in buffer zones were not visited during marking periods. A minimum marking length of 32 mm was selected because it was the minimum length at which a fish could be easily marked. We measured total length (TL) for all captured fish and fish with length $\geq$32 mm were marked using a combination of visual implant elastomer marks and pelvic fin clips. Elastomer marks represented the habitat of capture and fin clips depicted the marking occasion. Elastomer marks were either red or yellow and placed either under the dorsal fin or at the caudal peduncle. Recaptured fish caught during marking events were recorded and released without being given a new mark. During recapture periods, we visited two sites located in each buffer region in addition to sites located within habitats. All fish $\geq$ 32 mm were inspected for a mark, and we recorded the gender, length, and mark for each recaptured fish.

Salt Creek is a popular tourist site in Death Valley National Park, so we selected gear that minimized disturbance and visual impacts to the surrounding environment. Unfortunately, variability in fish behavior and microhabitat characteristics (e.g., substrate, depth, and aquatic vegetation) precluded the use of a single sampling gear in all habitats. Therefore, the choice of sampling gear for a particular site was determined by water depth. Specifically, lift nets were used in extremely shallow habitats ($<$5 cm), box traps were used in habitats 2–20 cm deep, and mesh traps were used in habitats with depths $>$20 cm. Lift nets were $1 \times 1\,m^2$ mesh quadrats ($<$1 mm mesh) attached to an external metal frame. Lift nets were placed on top of the substrate, and lifted upwards with a 3 m wooden pole after fish had settled on top of the mesh quadrat. Box traps were constructed from 7 mm hardware cloth lined with door screening ($<$2 mm mesh). Box traps had two rectangular-shaped openings ~3 cm wide. Mesh traps were collapsible minnow traps with 5 cm diameter openings and 3 mm mesh. Mesh traps were the primary sampling gear in the headwaters, both mesh and box traps were used in wetland and confined habitats, and box traps and lift nets were used in the braided habitat. Lift nets and box traps were fished actively in the braided habitat, and box traps and mesh traps were used as passive gears in all other habitats. Comparisons of size selectivity across sampling gears indicated no significant difference in mean lengths of fish captured in box traps and mesh traps ($t_{37.6} = 1.50$; $p = 0.14$), nor box traps and lift nets ($F_{1,1296} = 0.18$; $p = 0.67$).

Statistical analyses

Recaptures were divided into two groups: 'movers' (fish that were recaptured in a habitat different from their marking habitat) and 'non-movers' (fish that were recaptured in their marking habitat). Movement rate was expressed as the proportion of recaptures that were movers (Roberts and Angermeier 2007). Because our sampling design included multiple re-visits to sites within the same day (i.e., multiple 'collections'), we could not claim that collections from the same site were independent. Therefore, we calculated the mean number of movers and non-movers per site for each recapture period and used these numbers as estimates of movers and non-movers, respectively. We then summed these estimates from all sites within a habitat for each recapture period. We assumed that recaptures from different sites were independent, and that recaptures from each habitat and sampling period were independent. We further assumed that movers and non-movers were equally catchable.

To test differences in downstream and upstream movement in the confined and braided habitats, we compared the mean number of movers to non-movers using a Cochran–Mantel–Haenszel (CMH) chi-square test (a chi-square test for replicate samples; Snedecor and Cochran 1980). To compare temporal movement patterns, we fit a linear regression model to movement rates for each recapture period. Due to the restrictions of our sampling design, demographic characteristics of movers and non-movers could not be quantitatively analyzed.

Results

In total, we marked 4512 pupfish. Marked fish in the braided, confined, wetland, and headwaters habitats represented 20.5%, 31.0%, 24.2%, and 24.3% of the total marked population, respectively. Median length and variance in length increased slightly upstream from the braided to the wetland region; however, median length in the headwaters was the smallest of the four habitats (Figure 1). Mean lengths and sex ratios varied over small spatial scales (Figures 2 and 3), with downstream reaches exhibiting a greater proportion of males.

We recaptured a total of 444 fish, with the greatest number of recaptures occurring in the headwaters, followed by confined, braided, and wetland regions (Table 1). Fish recaptured in a habitat different from where they were marked (i.e., movers) comprised 10.8% of total recaptures, or 14.6% when including recaptures that moved into buffer regions. Movement, when detected, occurred between braided and confined habitats except in six recaptured fish. Of these six individuals, two fish moved from the braided to wetland habitat, two moved from the wetland to the confined habitat, one moved from the braided to the confined–wetland buffer region, and one moved from the confined to the confined–wetland buffer region (Table 1). A 38 mm male and a 36 mm female moved the longest observed distances from between the braided and wetland regions (>1.2 km).

As we only detected limited movement in wetland and headwater habitats, we limited our analyses to movement between downstream habitats (i.e., between the confined and braided habitats). Movers comprised 29.1% of total recaptures from the downstream habitats. Upstream and downstream movement rates between braided and confined habitats were not different (CMH statistic $= 1.65$; $p = 0.20$).

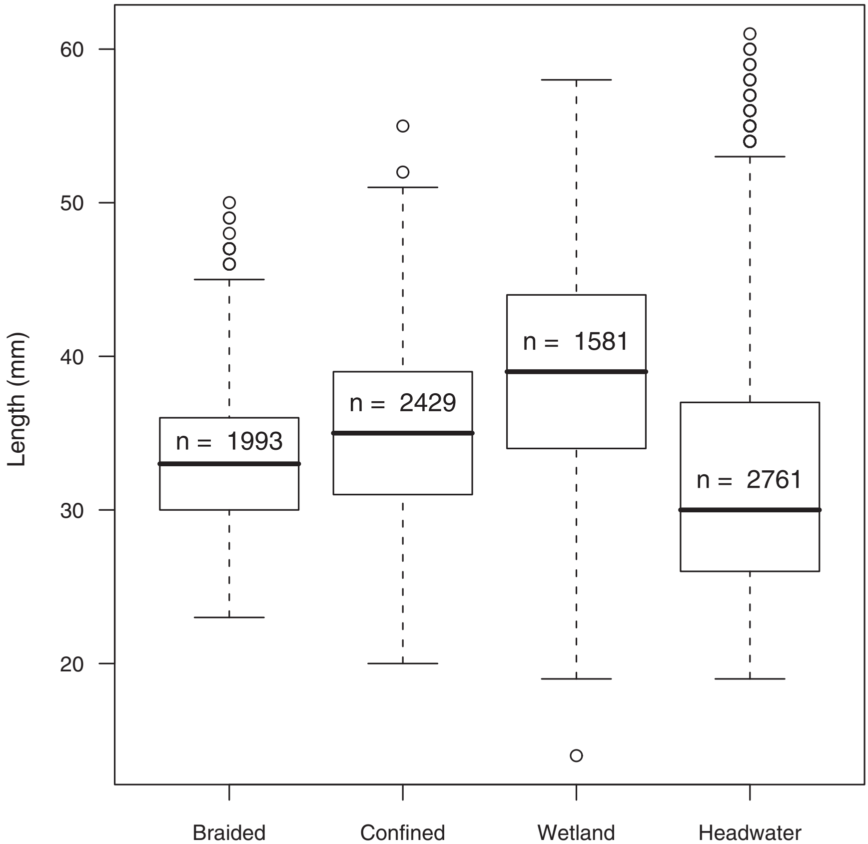

Figure 1. Length distributions of Salt Creek pupfish, *C. salinus salinus*, in braided, confined, wetland, and headwater habitats in Salt Creek, Death Valley National Park, CA, USA.

Similarly, we did not detect any temporal patterns in movement ($r^2 = 0.02$; $p = 0.32$), nor did we observe any patterns in sex ratios or lengths of movers (Figure 4).

Discussion

Mean lengths and sex ratios of Salt Creek pupfish varied over small spatial scales. Despite small-scale variability in median length among sites, median length increased upstream from the braided region to the wetland region. Interestingly, sex ratios of this study differ from those of Sada and Deacon (1995). In particular, Sada and Deacon (1995) documented sex ratios in all sampling sites to be predominantly female, with the exception of the downstream habitat, which exhibited an equal proportion of females and males. Sex ratio dissimilarity between Sada and Deacon (1995) and our study might be attributed to different sampling sites or sampling gear. Analogous to this study, Kodric-Brown's (1977) study of *Cyprinodon* spp. in Mirror Lake, NM, documented different behaviors and habitat preferences in males and females. Specifically, Kodric-Brown observed that while males spent diurnal hours defending breeding habitats located on limestone rock, female *Cyprinodon* only

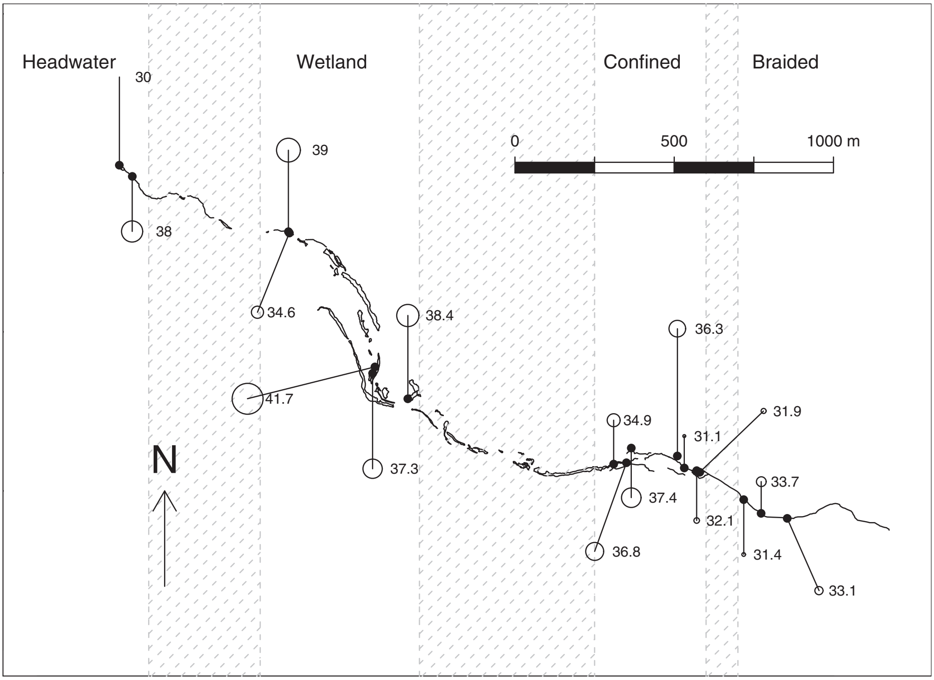

Figure 2. Sampling sites along Salt Creek, Death Valley National Park, CA, USA exhibited variability in mean length (mm) of Salt Creek pupfish (*C. salinus salinus*).
Notes: Sizes of open circles are proportional to mean length of fish captured at a sampling site. Numbers adjacent to open circles depict mean length of fish captured at the sampling site in millimeters. Habitats are listed along the top margin of the figure, and areas with gray cross-hatching represent buffer regions.

visited breeding habitats when ready to deposit eggs. We speculate that, in this study, differences in breeding behavior may have influenced sex ratios of sampling sites in Salt Creek.

Other studies assessing fish movement in lotic environments have observed that although most individuals within a population remain sedentary, some individuals will move long distances (Fraser et al. 2001; Rodríguez 2002). Consequently, movement patterns are best described by dividing the population into two categories representing mobile and stationary individuals. Similarly, whereas most individuals in this study did not move long distances during the spring breeding season, there were some exceptions. Namely, two fish which were recaptured >1.2 km away from their marking habitat. Importantly, because mark–recapture studies that re-visit marking sites may preferentially sample sedentary individuals (Gowan et al. 1994; Albanese et al. 2003), our estimates of movement rates are conservative.

We did not detect any movement into or out of the headwaters during the course of the study, suggesting that either fish emigration from the headwaters occurs during other times of year or emigration from the headwaters is rare. Furthermore, while downstream reaches slowly evaporated during the course of our study, we did not detect a temporal increase in upstream movement. Studies evaluating movement patterns of small-bodied fishes inhabiting intermittent streams provide mixed evidence as to effects of flow on movement (Labbe and Fausch 2000; Magoulick and

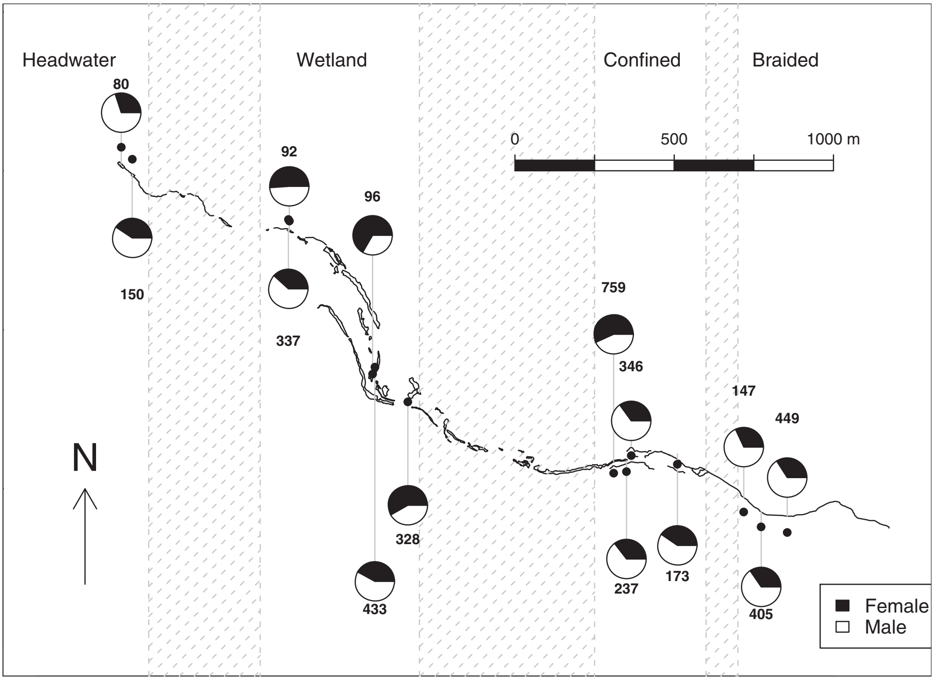

Figure 3. Sex ratios of Salt Creek pupfish, *C. salinus salinus*, varied among sampling sites along Salt Creek, Death Valley National Park, CA, USA.
Notes: As small fish were difficult to sex, pie charts depict sex ratios of fish with TL longer than 32 mm. Numbers near each pie chart represent sample size. Habitats are listed along the top margin of the figure, and areas with gray cross-hatching represent buffer regions.

Table 1. Number of Salt Creek pupfish (*C. salinus salinus*) recaptured in Salt Creek, Death Valley National Park, CA, USA.

	Marking habitat				
Capture habitat	Braided	Confined	Wetland	Headwater	Total
Braided	51	16	0	0	67
Braided–Confined	6	9	0	0	15
Confined	28	56	2	0	86
Confined–Wetland	1	1	0	0	2
Wetland	2	0	49	0	51
Wetland–Headwater	0	0	0	0	0
Headwater	0	0	0	223	223
Total	88	82	51	223	444

Note: Numbers of recaptures include both fish recaptured during recapture sessions and fish with marks from a previous marking session recaptured during marking sessions.

Kobza 2003; Albanese et al. 2004; Davey and Kelly 2007). Spring 2010 was uncharacteristically cool and wet for Death Valley, and the evaporation of Salt Creek was slow. As such, the braided region had not yet completely evaporated by mid-May at the conclusion of sampling.

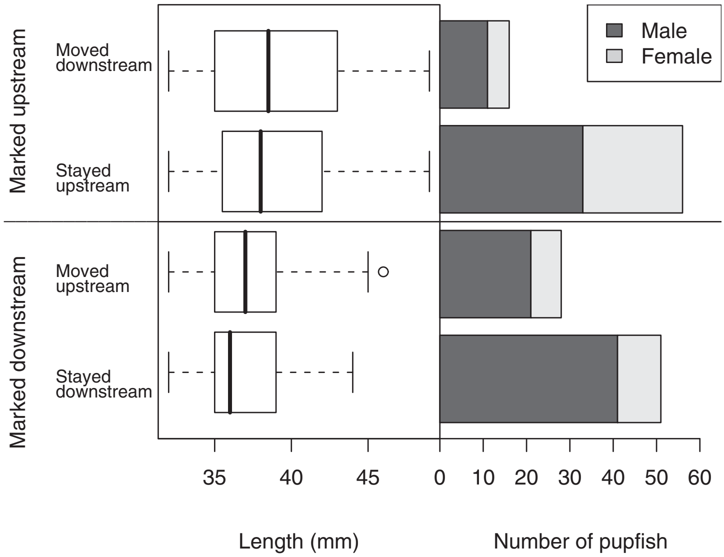

Figure 4. Length distributions (left) and sex ratios (right) of recaptured Salt Creek pupfish, *C. salinus salinus*, inhabiting Salt Creek, Death Valley National Park, CA, USA.
Notes: Demographic characteristics were compared between fish that moved (i.e., fish recaptured in a habitat that differed from the habitat in which they were marked) and fish that stayed (i.e., were recaptured in the same habitat in which they were marked).

While our study did not document substantial patterns in coarse-scale longitudinal movements across Salt Creek, movement between the two most downstream habitats was fairly common. Barlow (1958) observed that desert pupfish *C. macularius* density in the Salton Sea was influenced by water temperature and differed in January and August. Specifically, fish moved between shallow and deep waters once in January and twice in August. In general, fish preferred warm waters in the morning and cooler waters at night. However, in August, water temperatures in the shallow waters exceeded 36.5°C, consequently causing fish to move to deeper waters in the afternoon. Although not formally assessed in this study, we speculate that Salt Creek pupfish movement between braided and confined habitats occurred in response to diurnal changes in temperature. Specifically, the braided region was often devoid of fish on cool mornings, but became more densely populated in afternoon as water temperatures increased.

Studies assessing relationships between length and movement distances have mixed results (Albanese et al. 2004; Belica and Rahel 2007; Roberts and Angermeier 2007; Albanese et al. 2009). In an experimental study assessing emigration of *C. macularius*, McMahon and Tash (1988) documented that small male fish were more likely to emigrate compared to large and/or female fish. In our study, however, we did not detect any differences in sex ratio or length of movers compared to non-movers. Importantly, sample size of movers was small and represented solely by fish collected in braided and confined habitats in spring. Accordingly, demographic effects on movement may differ according to time of year and habitat.

Our observations suggest that breeding biology of Salt Creek pupfish is complex and influenced by spatio-temporal environmental conditions. Namely, phenology of breeding behavior differed among sites and territorial behavior was only observed at certain sites. Interestingly, in the confined habitat, the first fish to develop breeding coloration and territorial behavior inhabited an isolated pool. Time-staggered breeding across microhabitats of Salt Creek might be an adaptation to dynamic environmental conditions. Similar to this study, Soltz and Naiman (1978) describe population-level differences in breeding behavior of Amargosa pupfish (*C. nevadensis*) in response to local environmental conditions. Influences of spatio-temporal differences in breeding on movement patterns was not investigated by this study, but is likely important.

In summary, this study did not detect substantial coarse-scale movements of Salt Creek pupfish during their spring breeding season in upstream habitats. However, movement between the two most downstream habitats was fairly common, indicating that spatial heterogeneity may influence pupfish movement. Labbe and Fausch (2000) argue that multiple spatial scales must be considered for conservation of fishes inhabiting dynamic environments. Results of our study suggest that small-scale movements of Salt Creek pupfish are likely important, and we speculate the large-scale movements promote genetic exchange and re-populate downstream reaches during cool months. Accordingly, the importance of various spatial scales may change seasonally. Further research assessing year-round movement patterns of Salt Creek pupfish would help illuminate the importance of long-distance movements. More detailed insight into movement patterns would be provided by individual marks, passive integrated transponder antennae, or radio telemetry, approaches which are currently impractical due to the small body size of Salt Creek pupfish. Additionally, understanding differences in survival and recruitment in different habitats in Salt Creek may help guide conservation efforts in the future, particularly in the light of climate change.

Acknowledgments

We thank the Death Valley Natural History Association (DVNHA) for helping fund this study. Candace Lieber (DVNHA) and David Blacker (DVNHA) were very helpful with logistics for the study. The study included an educational outreach component, organized by the National Park Service (NPS) and partly funded by DVNHA, which educated 244 elementary and high school students about Salt Creek pupfish ecology in Death Valley National Park. S. Kyriazis (NPS) helped organize educational curriculum for students. In addition, we are grateful for the help of K. Wilson (NPS). We thank numerous volunteers who helped with field sampling, including: D. Wyatt, S. Kyriazis (NPS), J. Snow (NPS), M. Tilman (NPS), J. Tilman (NPS), J. Stoltzfus (NPS), P. Slaton (NPS), V. Schultz, and L. Finn (NPS). Furthermore, J. Stark (NPS) provided help with GIS mapping of Salt Creek. S. Parmenter (California Department of Fish and Game) provided biological insight and helped with permitting. This study was conducted under the California Department of Fish and Game permit number 803089-02, and NPS permit number DEVA-2009-SCI-0038. The Idaho Cooperative Fish and Wildlife Research Unit is jointly sponsored by the University of Idaho, US Geological Survey, Idaho Department of Fish and Game, and Wildlife Management Institute. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

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