

MOVEMENT PATTERNS OF *ETHEOSTOMA FONTICOLA* IN A HEADWATER
STREAM

THESIS

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by

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CHAPTER I

MOVEMENT PATTERNS OF *ETHEOSTOMA FONTICOLA* IN A HEADWATER STREAM

INTRODUCTION

Instream movement is a critical aspect of freshwater fishes life histories and enables populations to persist in lotic systems under variable ecological conditions (Meffe 1984), to maintain genetic connectivity and reproductive needs (Hall et al. 1991, Johnston 2000, Hutchings & Gerber 2002), and to recolonize areas following episodes of spates or dewatering (Labbe & Fausch 2000). Non-migratory stream fishes (i.e., resident fishes) generally move small distances (< 50 m) within creeks and small streams (Gerking 1953). Described initially by Gerking (1959), the restricted movement paradigm is applicable to a diverse group of resident fishes throughout southeastern and midwestern North American creeks and streams, including cyprinids (Johnston 2000; Belica & Rahel 2008), cottids (Brown & Downhower 1982; Petty & Grossman 2004), centrarchids (Gerking 1953), and percids (Freeman 1995; Roberts & Angermeier 2007). Methodologies in assessing instream movement and testing for congruency with the restricted movement paradigm have changed through time, specifically in study designs to remove bias associated with sampling shorter distances more frequently than longer distances from initial site of capture (Gowan et al. 1994; Albanese et al. 2003; Roberts et

al. 2008). Also, restricted movement paradigm has been expanded to include heterogeneity in movement by small proportions of conspecifics within high site fidelity populations (Smithson & Johnston 1999; Skalski & Gilliam 2000; Roberts et al. 2008; Breen et al. 2009). Regardless of distance moved, abiotic and biotic factors associated with instream movement include discharge intermittency, habitat type, habitat arrangement, sex, reproductive condition, body size, and predation threat (Gilliam & Fraser 2001; Croft et al. 2003; Albanese et al. 2004; Petty & Grossman 2004; Belica & Rahel 2008).

Patterns in movement recently have been described for some of the least mobile freshwater fishes, such as cottids (*Cottus gobio*, *C. girardi*; Knaepkens et al. 2004; Hudy & Shiflet 2009) and percids (*Etheostoma flabellare*, *E. podostemone*, *Percina roanoka*; Roberts & Angermeier 2007). *Etheostoma* represents a diverse lineage ($N = 128$; Page 2000) of small-bodied, benthic-oriented percids lacking a swimbladder (Evans & Page 2003). Currently, 44% (84 of 191) of percids are considered imperiled as a result of habitat degradation which includes dewatering, impacts of exotic species, stream altering water control structures, and habitat destruction (Jelks et al. 2008). Consequently, understanding instream movement is important to assess anthropogenic alterations and influences on species confined to a limited range. To date, available information suggests that *Etheostoma* exhibit high site fidelity in riffle habitats of southeastern streams (Roberts & Angermeier 2007) and in prairie streams within the Arkansas River basin (Labbe & Fausch 2000). However, at least one species is known to travel large distances (> 3 km) in southeastern streams to upstream spawning sites located in spring seeps (Boschung & Nieland 1986). Most species of *Etheostoma* reside in habitat highly

influenced by abiotic changes; consequently, little is known about movement in species that reside in relatively thermally-stable spring dominated rivers. The purpose of this study is to describe movement of *Etheostoma fonticola* (subgenus *Microperca*) in a spring dominated headwater stream of the Edwards Plateau in central Texas.

Etheostoma fonticola is the smallest darter, becoming sexually mature at 24 mm TL (Schenck & Whiteside 1977) and a maximum size of 36 mm SL (Page & Burr 1979). Mature ova are present in *E. fonticola* year round with likely peaks in spawning during summer and late winter (Schenck & Whiteside 1977) and, as with the other species of *Microperca*, they inhabit vegetated areas in slow-moving water, and eggs are found attached to vegetation (Page 1983; unpublished data, Phillips et al., US FWS). However, *E. fonticola* has the smallest distribution of the subgenus and is found only in two headwater streams of central Texas, San Marcos River and Comal River. In addition, instream flows of these rivers are highly dependent on groundwater contributions from the Edwards Aquifer (Crowe & Sharp 1997). Consequently, groundwater depletions along with periods of low rainfall are a pervasive threat to the persistence of the species (Linam 1993), prompting US Fish and Wildlife to list the fish as endangered in 1970 (U.S. Office of the Federal Register 35: 16047). Current threats not only include dewatering, through groundwater extraction, and lower instream flows, but recreational activities (swimming, wading, floating) and several dams in San Marcos and Comal rivers alter instream habitat and restrict gene flow. Regardless of the source of disturbance, understanding patterns in movement would provide necessary information to mitigate or lessen human impacts on the species. Specific objectives of this study were to test for site fidelity, to quantify directionality and magnitude of movement, and to assess

factors associated with movement for *E. fonticola* located in the spring dominated Comal River.

METHODS

Study area

The Comal River is located in central Texas along the Balcones Fault Zone of the Edwards Plateau and is in a highly urbanized watershed (Fig. 1). As with many Edwards Plateau rivers, base flows are supported by groundwater discharges from the Edwards Aquifer and, therefore, maintained at nearly constant water temperatures and other chemical and physical environmental conditions year round (Groeger et al. 1997). Instream structures regulate stream discharge and create Landa Lake, which is the headwaters of Comal River, and are located throughout entire stream system. Discharge from Landa Lake enters either the old or new channel and is controlled by instream structures which shunt a majority of spring flow towards the new channel. The Comal River system is characterized by a generally stable hydrograph temporally with a monthly mean discharge (1938-2009) of $8.5 \pm 0.13 \text{ m}^3/\text{s}$ (mean \pm SE). However, shorter duration (years to decades) disturbance events (i.e. drought) are a major threat to in-stream flows. Under increased pressure generated by groundwater extraction from the Edwards Aquifer (321,000 acre-feet / year) as well as the drought of record, Comal Springs ceased to flow for a period of 5 months in 1956 (Brune 2002). Subsequent to this event the fountain darter was considered extirpated from the system and was later reintroduced with 457 individuals from San Marcos River stock by Southwest Texas State University personnel (Schenck & Whiteside 1976). Since the 1950's, pressure on the aquifer from

anthropogenic sources has increased, but has been tempered by the regulation of groundwater resources in the Edwards Aquifer. However, by state law, the Edwards Aquifer Authority (regulatory body) must permit no less than 340,000 acre-feet for each calendar year (EAA 2010), so that cessation of discharge from Comal Springs should be expected in a drought as severe as experienced in the 1950's. These types of disturbance events and resulting abiotic and biotic fluctuations are the most pervasive threat to the survival of the fountain darter. This study was conducted in a 200 m reach of the old channel of the Comal River (29° 42' 39.66" W; 98° 07' 40.52" N). This area was selected because it was characterized by several vegetation types and a single geomorphic unit (run) which is typical of the species current range. In addition, this area supports a sufficient population of fountain darters, estimated (95% CI) at 2,732 (2,012 – 4,254) individuals (Appendix 1).

Study design

Mark-recapture methods were used to evaluate the movement patterns of the fountain darter. The 200-m reach was divided into three sections: 100-m core section for marking and searching, and 50-m upper and lower sections for searching only. Dominant and subdominant vegetation were mapped to establish sampling replicates and were continuously monitored throughout the duration of the study. Non-vegetated substrate was excluded as a sampling unit as the fountain darter is rarely found in these areas (Schenck & Whiteside 1976; Linam 1993). Dominant and subdominant vegetation in the study reach included *Hygrophila polysperma* and *Ludwigia repens* (combined as one vegetation type based on similar growth forms and referred to as *H. polysperma*

throughout), *Riccia fluitans* and a filamentous algae (*Rhizoclonium* sp.). *Hygrophila polysperma* is a rooted macrophyte that extends through the water column, whereas *R. fluitans* and filamentous algae generally limit growth to only a few centimeters above the substrate.

The study reach was stratified based on vegetation type: *H. polysperma*, *H. polysperma* with *R. fluitans* (referred to as mixed stands of *H. polysperma* throughout), *R. fluitans* and filamentous algae. Four replicates of each vegetation type, when available, were randomly selected in the 100-m core reach for sampling. In addition, two replicates of each vegetation type were randomly selected and sampled in the 50-m upstream and downstream reaches. Areas of contiguous vegetation $>40 \text{ m}^2$ were subdivided into approximately 20 m^2 sub-units and each was treated as an individual unit for selection purposes. The midpoint of each sampling replicate was established through GIS methods using a Trimble GeoXT (Trimble, Sunnyvale, CA, USA) and Arcmap (ESRI, Redlands, CA, USA) to maintain a permanent record of replicate locations and obtain distances between each pair of replicates. Quadrats within each sampling replicate were established to capture fountain darters. Effort to capture fountain darters within quadrats was standardized with the use of a drop net. The drop net consists of 1-mm mesh netting connected to a 2 m^2 frame extending through the water column to isolate a defined area. A depletion method was implemented by sweeping the isolated area with a dip net until no darters were captured after three successive attempts. At each replicate, quadrats were established at a density of approximately one quadrat per 5 m^2 of available habitat. Sampling replicates were limited to a 20 m^2 area, even when replicates were greater than 20 m^2 . At each quadrat and during each sampling event, depth (cm), instantaneous flow

(cm/sec; Flo-mate 2000, Hatch Environmental, Loveland, CO, USA), pH, temperature (°C) and dissolved oxygen (mg/l; Hydrolab, Hatch Environmental, Loveland, CO, USA) were measured.

From August 2008 to June 2009, nine field collections were made monthly among three seasons (summer-fall: August – October, winter: December – February, spring-summer: April-June). Year round collections were purposely avoided to minimize effects of sampling on available habitat and biota while retaining seasonal information. Captured fountain darters were anesthetized in a 60-mg/L solution of tricaine methanesulfonate (MS-222; Finquel, Argent Chemical Laboratories, Inc., Redmond, Washington). Sex and total length (TL, mm) were obtained, and darters > 20-mm TL were marked with a unique batch mark to reference time and location (replication) of collection. Fish were marked using visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington, U.S.A.) as this method is well-suited for marking small-bodied fishes. Visible implant elastomer has high retention in fountain darters and there was no observed effects on survival and growth in a laboratory study (Phillips & Fries 2009). Two marks were injected into each darter among five body locations (left and right anterior dorsal fin proximal base, left and right ventral muscle tissue and caudal peduncle) and with one or two of four possible color combinations. Established protocols for marking fountain darters were followed using a BD 0.3 cc insulin syringe with a 29 gauge needle (Northwest Marine Technology, Shaw Island, WA, USA). Darters were held in fresh river water until full recovery from anesthetic and then released in the sampling replicate from where they were captured.

Data analysis

Distance moved by recaptured fish was measured as the distance (m) between midpoints of sampling replicates. This measurement was an estimate of net distance moved over a time interval, representing population redistribution at a point in time and not total distance moved by an individual. Individuals recaptured in the same sampling replicate as initial capture were classified as non-movers and assigned a movement distance of 0 m. Mean distance moved by recaptured fish was determined for all fish and only fish classified as movers with respect to direction. Positive values were assigned to upstream movements and negative values assigned to downstream movements. Estimate of directional bias in movement was assessed through a t-test of a single mean (Turchin 1998). Mean distance moved was determined for non-movers with upstream movers and non-movers with downstream movers to account for potential bias in movement direction. Mean distance moved was determined for the absolute value of distance moved for all fish and only fish classified as movers.

Fidelity to the site of initial capture was assessed by comparing the mean distance moved by recaptured fish with the mean distance observable. Mean distance observable was defined as the mean distance between each pair of sampling replicates in the core reach. A common criticism of mark-recapture studies is that a systematic bias is introduced to the analysis by study design which is a result of shorter movement distances that are sampled with greater frequency than longer distances (Albanese et al. 2003). This is evident in this study where 23% of pairs of sampling patches could reveal movement distances < 10 m while only 3% could reveal a movement > 90 m. Therefore, randomization tests were used to compare the mean of the distribution of observable

movement distances with the mean of the distribution of distances moved by recaptured fish. By considering only the observable distances, and therefore the frequency of observable distances, the bias introduced through study design is incorporated into the data analysis so that the question of restricted movement can be objectively addressed (Roberts et al. 2008).

Logistic regression was used to identify factors associated with the movement decisions of individual fish. Four independent variables that can have an effect on movement decisions, established from the literature, were evaluated. These variables included the season of recapture, sex, body size (TL), and time elapsed between marking and recapture. The dependent variable for all models was the probability of an individual leaving the patch of initial capture. Models for comparison were built by combining the four independent variables, as well as, a null model for a total of 16 candidate models. Akaike's Information Criteria corrected for small sample size (AIC_c) was used to evaluate models. The difference in AIC_c (ΔAIC_c) values was used as a measure of support for each model relative to the best model from the available data. Models with a $\Delta AIC_c < 2$ are considered to have substantial support while models with a $\Delta AIC_c > 7$ are generally thought to have very little support and essentially no support when $\Delta AIC_c > 10$ (Burnham & Anderson 2002). The model with the minimum AIC_c was interpreted for the influence of independent variables, which appeared in this model, on the probability of an individual leaving the replicate of initial capture.

Analysis of variance (ANOVA) was used to evaluate the effect of these independent variables on the distance moved by those fish classified as movers. Season was withheld from this analysis as a result of small sample size. Distance moved was log

transformed prior to analysis to meet the assumption of a normally distributed dependent variable. Models were evaluated using AIC_c as described above. All statistical procedures were carried out using the program R (version 2.9.1; R Development Core Team 2005).

RESULTS

Habitat use

Four hundred thirty-four quadrats were established in vegetated habitats. *Riccia fluitans* and *H. polysperma* were the most commonly sampled habitats throughout the study reach (28% each) followed by mixed stands of *H. polysperma* with *R. fluitans* (24%) and algae (21%; Table 1). Availability of each vegetation type varied temporally among seasons (ranges: 25-31% for *H. polysperma*, 26-30% for *R. fluitans*, 22-28% for mixed *H. polysperma*, and 15-24% for algae), but total sampling effort among vegetation types did not differ (across seasons: $\chi^2_3 = 7.0$, $P = 0.07$; within seasons: $\chi^2_{11} = 12.8$, $P = 0.31$). Mean (1 SE) water depth was 78 (11) cm among habitats and ranged from 49 (5) cm in algal habitats to 102 (4) cm in *R. fluitans* habitats. Mean current velocity was 7 (2) cm/s and ranged from 3 (0) cm/s in algal habitats to 12 (1) cm/s in *H. polysperma* habitats (Table 1). Otherwise, abiotic variables (i.e., dissolved oxygen, pH, and water temperature) varied little among habitats and through time because of the relatively stable hydrograph between September 2008 (1.6 m³/s) to May 2009 (1.4 m³/s). Mean water temperature was 23.6 (0.7) °C and ranged from 22.2 (0.1) °C in winter to 24.3 (0.1) °C in spring-summer, mean pH was 7.2 (0.1) and ranged from 7.1 (0.0) in the summer-fall to

7.4 (0.0) in the winter, and mean dissolved oxygen was 8.3 (0.8) and ranged from 7.1 (0.0) in the summer-fall to 9.9 (0.1) in the winter.

A total of 1,103 fountain darters was captured. Fountain darters ≤ 20 mm in TL ($N = 105$) were released without marking. Sixty-eight percent of darters ≤ 20 mm in TL were captured during spring-summer, 31% captured in summer-fall, and 1% in winter. Fountain darters > 20 mm in TL ($N = 942$) were captured, marked, and released from all vegetation types. During the final sampling period 56 additional darters were captured but not marked, and approximately 150 opportunistically captured outside of the study reach, from a likely barrier to movement upstream (culvert at road crossing) to the confluence with the new channel downstream. Mean (1 SD) total length of darters > 20 mm in TL was 29 (1) mm ($N = 998$), 28 (4) mm for female darters ($N = 488$), and 30 (3) mm for male darters ($N = 510$). Sex ratio did not differ ($\chi^2_1 = 0.02$, $P = 0.49$) from 1:1. Highest percentages of fountain darters were marked and released in *R. fluitans* (44%) and algae (39%), followed by mixed stands of *H. polysperma* (13%), and *H. polysperma* (4%; Fig. 2). Mean (1 SE) darter density was 1.3 (0.5) darters/m² and ranged from 0.3 (0.1) darters/m² in *H. polysperma* to 2.2 (0.3) darters/m² in algae (Table 1).

A total of 942 darters was marked and 8.7% of those were recaptured. Mean (1 SD) total length was 30 (1) mm for all recaptured individuals, 30 (3) mm for females ($N = 50$) and 30 (3) mm for males ($N = 32$). Highest percentages of recaptured darters were collected in algae (52%) and *R. fluitans* (32%), followed by mixed stands of *H. polysperma* (15%), and *H. polysperma* (1%). Seasonally, recaptured darters ranged from 48% during summer-fall to 59% in algal habitats during spring, 14% during winter to 43% during summer-fall in *R. fluitans*, 9% during spring-summer to 24% during winter

in mixed stands of *H. polysperma*, and 0% during summer-fall and spring-summer to 3% during winter in *H. polysperma*. Proportions of darters captured in each vegetation type differed between initial capture and recapture events when pooled across season ($\chi^2_3 = 11.7$, $P < 0.01$; Fig. 3) but did not differ within season ($\chi^2_9 = 14.9$, $P = 0.09$; Fig. 4). Sixty-one percent ($N = 82$) of the darters were recaptured in the same habitat as initial capture and 39% were found in a different vegetation type. Fish classified as non-movers ($N = 40$) were captured from algae or *R. fluitans*. Among fish classified as movers that moved among the same vegetation type, 90% ($N = 10$) were found in algae or *R. fluitans*, and 32 individuals moved into different habitat than original capture: 50% moved into algae habitats, 13% into *R. fluitans* habitats, 34% into mixed stands of *H. polysperma*, and 3% into *H. polysperma*.

Movement

Mean (1 SD) distance of recaptured fountain darter movement ($N = 82$), incorporating direction of movement, was 6 (19) m upstream, and 12 (25) m upstream excluding non-movers ($N = 42$). Movement was biased in an upstream direction ($t = 2.90$, $P < 0.01$, d.f. = 81) with 81% of darters classified as movers directed upstream and 19% moving downstream (Fig. 5). Mean distance of darters moving upstream including non-movers was 9 (16) m, and 4 (10) m for downstream movers with non-movers. Irrespective of direction, fountain darter movement was 10 (17) m for all recaptured fish and 20 (18) m excluding non-movers (Table 2). The maximum distance moved by an individual was 95 m over a 26 day interval. Distances of fountain darter movement among all fish, movers only, and upstream or downstream movers were less than the

mean detectable movement. Mean detectable movement distance within the reach was 35 (27) m and was greater than mean distance of fountain darter movement of all recaptured fish (mean: 10 (17) m; empirical $P < 0.01$; $N = 82$) and movers only (20 (18) m; empirical $P < 0.01$; $N = 42$), upstream movers and non-movers (9 (16) m; empirical $P < 0.01$; $N = 74$), and downstream movers and non-movers (4 (10) m; empirical $P < 0.01$; $N = 48$; Fig. 6).

Probability of fountain darter movement was influenced by both season and TL (Fig. 7; Table 3). The odds of an individual moving from the replicate of initial capture were 4.1 times greater in winter ($z = 2.5$, $P = 0.01$, d.f. = 77) and 2.3 times greater in spring ($z = 0.8$, $P = 0.41$, d.f. = 77) as opposed to fall (Table 4). The proportion of individuals classified as movers (52%; $N = 82$) was 36% ($N = 42$) in fall, 72% ($N = 29$) in winter, and 55% ($N = 11$) in spring. The odds of a darter moving from the replicate of initial capture were 1.2 times greater for every increase of 1 mm in TL ($z = 1.9$, $P = 0.06$, d.f. = 77) with smaller fish (< 30 mm; mean TL) classified as movers (32%; $N = 31$) less frequently than larger (≥ 30 mm) fish (64%; $N = 50$). There was no detectable effect of sex, TL, or elapsed time on distance moved by individuals (Table 5).

DISCUSSION

Fountain darters exhibited high site fidelity within the study area. Even individuals that moved among habitat replicates exhibited high site fidelity, meaning movement of individuals was less than what would be expected if individuals were not restricting movement throughout the area. High site fidelity observed in this study might be attributed, in part, to habitat quality. Fountain darters are more heavily associated

with low growing aquatic vegetation which might represent higher quality habitat (Schenck & Whiteside 1976; Linam et al. 1993), presumably, as with other stream fishes, high quality habitat provides cover from predators (Savino & Stein 1982), foraging opportunities, and suitable spawning sites (Petty & Grossman 2004; Roberts & Angermeier 2007). All individuals classified as non-movers were taken from either algae or *R. fluitans* habitats, which form dense mats close to the substrate, and 69% of individuals classified as movers were taken from either algae or *R. fluitans*. Availability of these and the other vegetation types persisted throughout the study. Roberts & Angermeier (2007) also related high site fidelity in *E. flabellare* and *E. podostemone* to stability of habitats. Conversely, movement rates increased for these species in response to decreased stability. Availability of adequate foraging and reproductive habitat is associated with high site fidelity among other benthic fishes (Roberts & Angermeier 2007; Breen et al. 2009). Obviously, water quality variables, such as water temperature and dissolved oxygen, must be within physiological tolerances of the species to promote site fidelity (Albanese et al. 2004).

Fountain darter movement was associated with season and body size. Among seasons, percentage of movers was highest in the winter (72%), followed by spring-summer (55%) and summer-fall (36%). Correspondingly, availability of algae and *R. fluitans*, which contained the highest densities of darters, was lower in the spring-summer (effort: 15% in algae; 26% in *R. fluitans*) and winter (20%; 28%) than in the summer-fall (24%; 30%). Fountain darter movement increased during periods of decreasing amounts of high quality habitat. This is consistent with other studies that found stream fish movement is correlated with availability of quality habitats (Gowan & Fausch 2002;

Roberts & Angermeier 2007). Reduced likelihood of movement for two species, blacknose dace (*Rhinichthys atratulus*) and torrent sucker (*Thoburnia rhotoecca*), in Virginia streams is associated with high-quality tributary habitats located further from lower quality main-stem habitat (Albanese et al. 2004). Alternatively, seasonal differences in fountain darter movement might be attributed to spawning events as indicated by the association of movement observed with body size. In this study, larger darters moved more often than smaller darters. Fountain darters are phytophils, spawning year round but with greater reproductive output during winter and summer (Schenck & Whiteside 1977). Furthermore, the large abundance and size of age-0 fish (mean TL: 17 mm, $N = 71$) in spring-summer suggest that a successful spawning event occurred in the winter sampling period, assuming a growth rate of 0.2 mm/d in laboratory trials (Brandt et al. 1993) is similar in wild populations. Collectively, more frequent movement of larger fountain darters during winter suggests a relationship between fish size and reproduction. Seasonality in movement patterns related to reproduction is common among riverine fishes, including salmonids, esocids, cyprinids, and percids (Boschung & Nieland 1986; Lucas & Batley 1996; Schlosser 1998; Ovidio & Philippart 2002; Acolas et al. 2006). This, in conjunction with quality habitat availability, might explain seasonal heterogeneity in fountain darter movement. As an interesting addendum, movement associated with reproduction might also explain the magnitude of movement found in the fountain darter. To maintain persistence in lotic systems, larval fish float downstream and juvenile through adult fish generally move upstream (Slack et al. 2004). Benthic-associated larvae, such as fountain darter larvae (Phillips, personal observation), tend to have shorter displacement distances than pelagic-associated larvae (Paine 1984; Turner

2001). Consequently, high site fidelity observed in this study suggests that large upstream movements might not be required to compensate for larval drift in the fountain darter population so long as suitable vegetation is available and water quality parameters are sufficient in the stream reach.

Maximum distance traversed by a fountain darter was 95 m within 26 days, and 7% of darters moved further than the mean observable distance. Individual centrarchids, cottids, cyprinids, and percids (Hill & Grossman 1987; Smithson & Johnston 1999; Roberts et al. 2008) move substantial distances from the initial point of capture although a majority of their respective populations exhibit high site fidelity. A small proportion, 3-9%, of percids in a Virginia stream moved longer distances than conspecifics that display high site fidelity (Roberts & Angermeier 2007). Leptokurtosis in movement distance distributions is attributed to movement heterogeneity among individuals within a population (Skalski & Gilliam 2000). Movement heterogeneity, specifically long distance movers, likely is genetic based (i.e., boldness; Fraser et al. 2001) and represents important aspects of population dynamics through time and space (Turchin 1998). Mobile individuals disperse at faster rates (Skalski & Gilliam 2000), and are likely the first to reach newly available or defaunated habitats (Scheurer et al. 2003) and areas of refugia during periods of duress (Labbe & Fausch 2000). These observations are supported experimentally in one species. Potomac sculpin (*Cottus girardi*), a benthic species with high site fidelity, were able to repopulate experimentally defaunated areas rapidly, likely as a result of a small percentage of a large population making longer movements (Hudy & Shifelt 2009). Consequently, maintaining conduits for movement is not only important for migratory species (i.e., mountain mullet, freshwater eels,

numerous cyprinids; Lee 1980; McDowall 1988; Skov 2008) but also for fishes that exhibit high site fidelity (Roberts & Angermeier 2007; Breen et al. 2009) to allow access in newly available habitat, previously defaunated habitat, and areas of refugia.

Connectivity of aquatic habitat is important for the long-term conservation of stream fishes (Labbe & Fausch 2000), even in the generally abiotically stable habitat found in spring-influence headwater reaches of the Edwards Plateau region. As demonstrated in this study, fountain darters exhibit high site fidelity but a small percentage exhibited high mobility. Though the importance of the high mobility is not known, it does demonstrate that fountain darters have the capacity to move distances to avoid areas dewatered or disturbed. Discharges in the Comal and San Marcos River systems are influenced by agriculture and groundwater pumping (Crowe & Sharp 1997). During the 1950s, Comal River ceased flowing during a 6-year period of below-average precipitation (Linam et al. 1993) which led to the extirpation of the fountain darter (Schenck & Whiteside 1976). Whether the fountain darter will move or not during periods of duress is not known and likely dependent on the amount and location of suitable habitat. However, the capacity to move suggests that fountain darter will need unimpeded stream reaches and continuous vegetated habitat corridors to make the movement to areas of refuge and to return to areas previously inhabited. Currently, numerous instream barriers are located in the Comal and San Marcos rivers and restrict fountain darter movement, at least to upstream areas. From a conservation perspective, consideration of removing or modify existing instream barriers to allow unimpeded access might benefit the fountain darter. Alternatively, instream barriers are being used to protect biotic integrity of some stream reaches by eliminating access from the non-

native fishes downstream (Jackson & Pringle 2010). Understanding the importance of fountain darter movement and how it benefits the genetic diversity and long-term viability of the species will be necessary before management actions are considered.

Table 1. Summary table of habitat characteristics including water quality parameters, sampling effort, and density of fountain darters. Sampling effort (# of quadrats and % of total effort) and mean (1 SE) density of fountain darters (fish / m²), depth (cm), current velocity (CV, cm / s), dissolved oxygen (DO, ppm), pH, and temperature (° C).

Vegetation type	Total effort	% of effort	Density	Depth	CV	DO	pH	Temp
Pooled								
Algae	89	21	2.2(0.3)	49(5)	3(0)	8.3(0.6)	7.2(0.1)	23.5(0.4)
<i>R. fluitans</i>	121	28	1.9(0.5)	102(4)	5(1)	8.3(0.5)	7.2(0.1)	23.5(0.4)
mixed <i>H. polysperma</i>	102	24	0.7(0.1)	76(4)	7(1)	8.3(0.5)	7.3(0.1)	23.6(0.4)
<i>H. polysperma</i>	122	28	0.3(0.1)	83(2)	12(1)	8.3(0.6)	7.2(0.1)	23.6(0.4)
Fall								
Algae	38	24	3.3(0.2)	53(3)	3(1)	7.1(0.2)	7.1(0.0)	24.2(0.1)
<i>R. fluitans</i>	47	30	3.6(0.8)	112(2)	6(1)	7.0(0.2)	7.1(0.0)	24.0(0.1)
mixed <i>H. polysperma</i>	34	22	1.1(0.2)	81(4)	8(2)	7.1(0.2)	7.1(0.0)	24.1(0.1)
<i>H. polysperma</i>	39	25	0.3(0.0)	83(4)	12(0)	7.1(0.5)	7.1(0.0)	24.3(0.3)
Winter								
Algae	29	20	1.2(0.3)	64(7)	3(1)	10.1(1.2)	7.5(0.1)	22.4(0.5)
<i>R. fluitans</i>	41	28	0.7(0.2)	89(8)	6(1)	9.7(1.1)	7.4(0.1)	22.1(0.5)
mixed <i>H. polysperma</i>	32	22	0.6(0.0)	80(9)	7(2)	9.8(1.1)	7.4(0.1)	22.2(0.5)
<i>H. polysperma</i>	43	30	0.2(0.0)	85(3)	11(2)	9.9(1.2)	7.4(0.1)	22.2(0.4)
Spring								
Algae	19	15	2.1(0.4)	31(3)	2(0)	7.8(0.4)	7.1(0.1)	23.9(0.5)
<i>R. fluitans</i>	33	26	1.4(0.2)	108(4)	4(1)	8.1(0.5)	7.2(0.1)	24.5(0.5)
mixed <i>H. polysperma</i>	36	28	0.5(0.0)	68(3)	5(1)	7.9(0.5)	7.4(0.2)	24.5(0.7)
<i>H. polysperma</i>	40	31	0.3(0.1)	82(2)	14(1)	8.0(0.5)	7.1(0.1)	24.2(0.4)

Table 2. Summary of distance moved by recaptured fountain darters. Mean (1 SD) distance of recaptured fountain darter movement considering direction, upstream and non-movers, downstream and non-movers, irrespective of direction, and maximum distance.

	Movement distance (m)		
	Directional	Non-directional	Maximum
All fish (<i>N</i> = 82)	6 (19) upstream	10 (17)	95
Movers only (<i>N</i> = 42)	12 (25) upstream	20 (18)	
Upstream movers and non-movers (<i>N</i> = 74)	9 (16)		
Downstream movers and non-movers (<i>N</i> = 48)	4 (10)		

Table 3. Candidate logistic regression models of fountain darter movement. Models listed with predictors, number of parameters estimated (K), log-likelihood, and ranked by Akaike Information Criteria corrected for small sample size. Interpreted model designated by asterisk.

model predictors	K	Log-Likelihood	AICc	Δ AICc	Akaike Wt
length, season	4	-48.76	106.05	0.00	0.18*
length, sex, season	5	-47.62	106.05	0.00	0.18
sex, season	4	-49.19	106.90	0.85	0.12
length, sex, time	4	-49.50	107.52	1.48	0.08
season	3	-50.70	107.71	1.66	0.08
length, time	3	-50.93	108.16	2.12	0.06
length	2	-52.06	108.28	2.23	0.06
length, time, season	5	-48.76	108.32	2.27	0.06
length, sex, time, season	6	-47.62	108.38	2.33	0.06
sex, time, season	5	-49.16	109.12	3.08	0.04
length, sex	4	-50.63	109.79	3.75	0.03
time, season	4	-50.67	109.87	3.83	0.03
sex, time	3	-51.78	109.88	3.83	0.03
time	2	-53.75	111.65	5.60	0.01
sex	2	-54.05	112.26	6.22	0.01
null	1	-56.09	114.23	8.18	0.00

Table 4. Summary of the logistic regression model selected by AIC_c for fountain darter movement including predictors (β), regression coefficients (estimate), standard error of estimate, z-value, and p-value.

β	Estimate	Std. Error	z value	p-value
Intercept	-5.76	2.80	-2.06	0.04
TL	0.18	0.09	1.87	0.06
Spring	0.58	0.70	0.83	0.41
Winter	1.41	0.56	2.50	0.01

Null deviance: 112.18 on 80 degrees of freedom

Residual deviance: 97.52 on 77 degrees of freedom

Table 5. Candidate linear regression models of distance moved by fountain darter movement distances with predictors, number of parameters estimated (K), log-likelihood, and ranked by Akaike Information Criteria corrected for small sample size.

model predictors	K	SSE	AICc	Δ AICc	Akaike Wt.
null	1	31.5	-10.0	0.0	0.32
time	2	30.5	-9.2	0.8	0.21
sex	2	31.1	-8.3	1.6	0.14
length	2	31.4	-7.9	2.1	0.11
sex, time	3	30.3	-7.1	2.8	0.08
length, time	3	30.4	-7.0	3.0	0.07
length, sex	3	31.1	-6.1	3.9	0.04
length, sex, time	4	30.2	-4.8	5.2	0.02

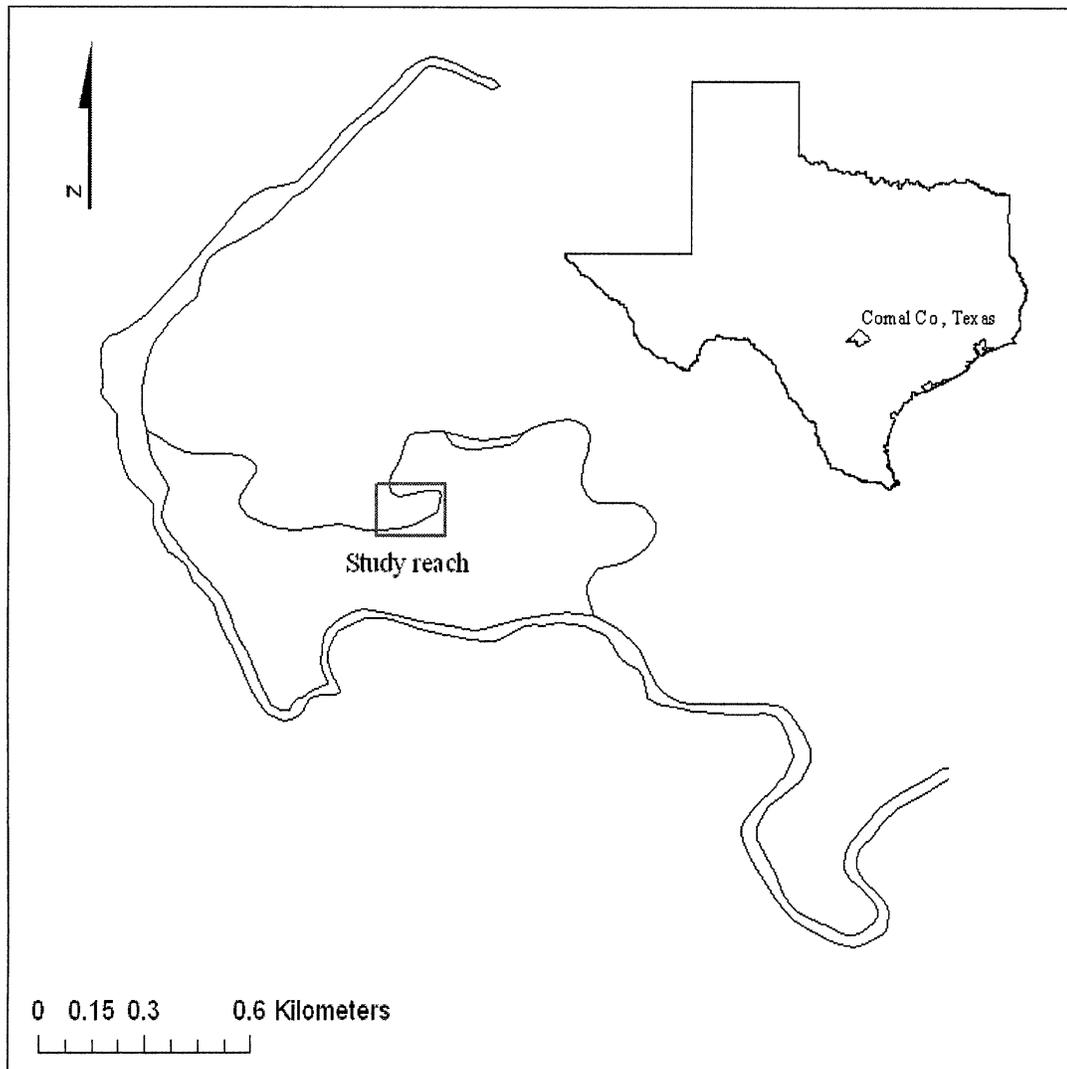


Fig. 1. Map of the Comal River from the headwaters to the confluence with the Guadalupe River located in Comal Co., Texas, U.S.A.

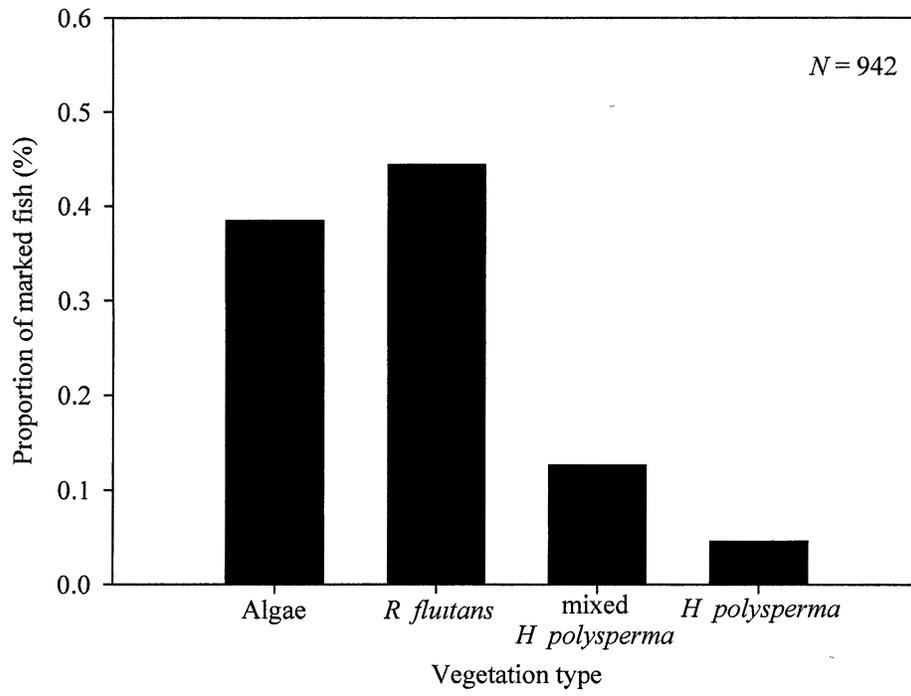


Fig. 2. Proportion of marked fountain darters by vegetation type.

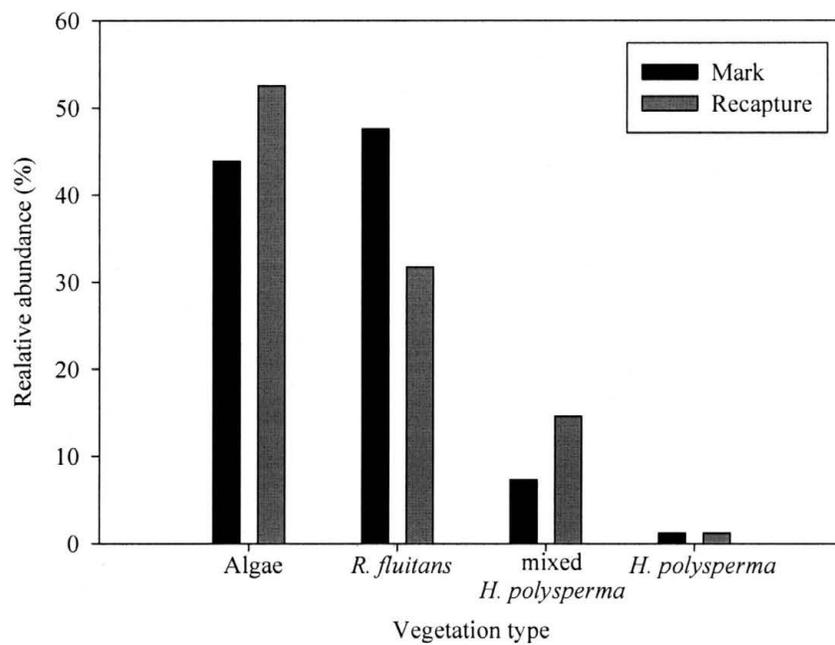


Fig. 3. Mark (black bars) versus recapture (gray bars) locations of fountain darters by vegetation type pooled across seasons ($N = 82$).

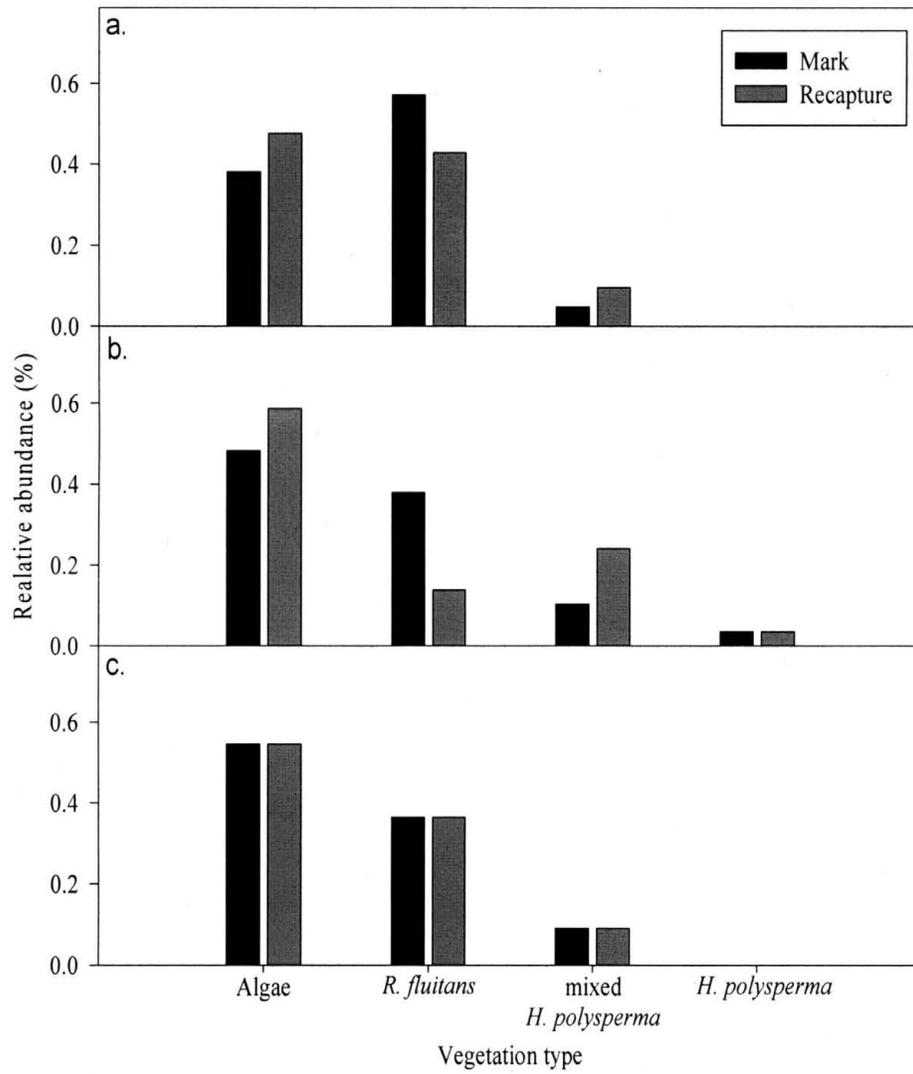


Fig. 4. Mark (black bars) versus recapture (gray bars) locations of fountain darters by vegetation type for (a.) summer-fall ($N = 42$), (b.) winter ($N = 28$), and (c.) spring-summer ($N = 11$).

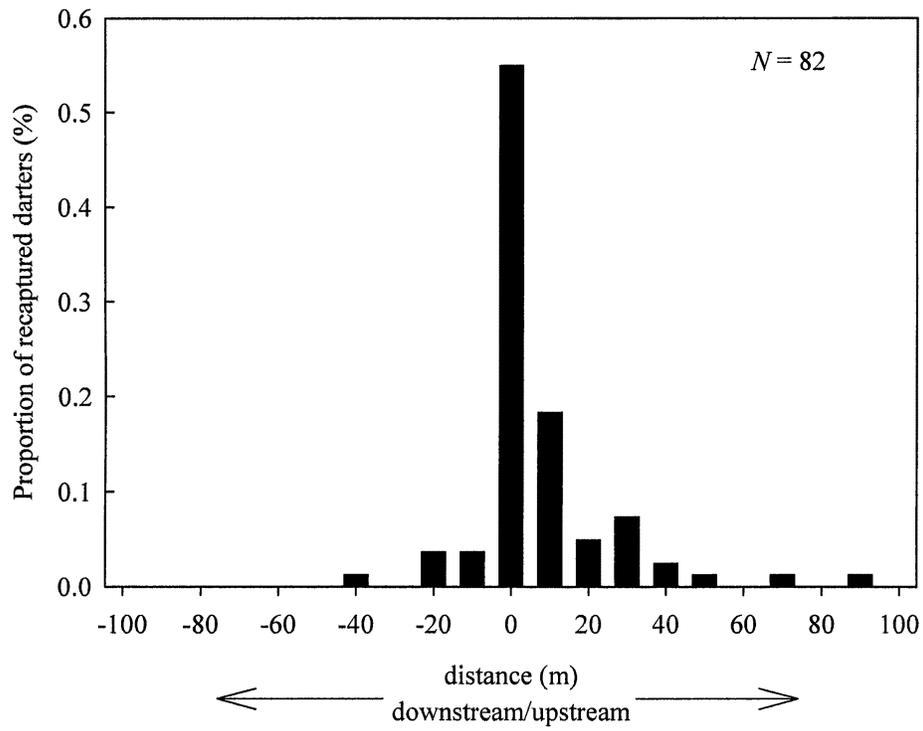


Fig. 5. Frequency distribution of movement distances (m) by fountain darters.

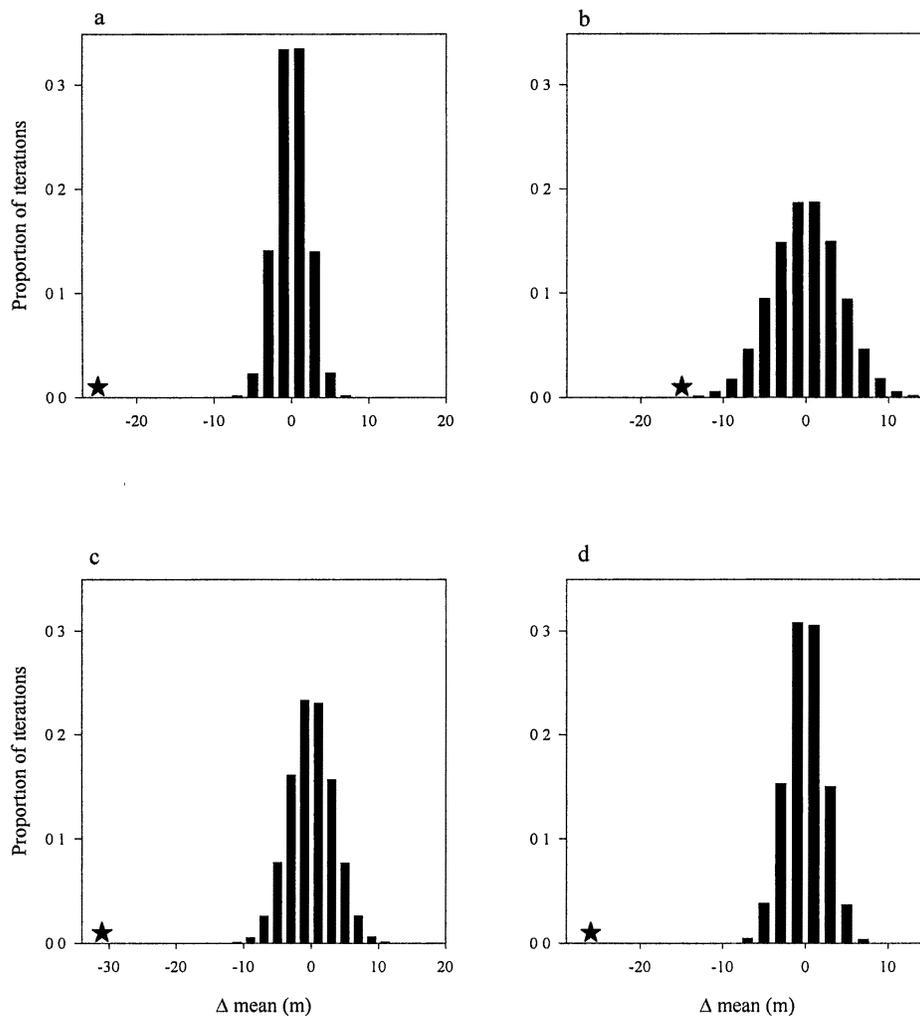


Fig. 6. Outcome of randomization tests to assess site fidelity. Frequency distribution of the difference between the mean observable distance (Δmean) and the 99,999 sample iterations from the randomization tests for (a.) movers and non-movers, (b.) movers only, (c.) downstream movers and non-movers, and (d.) upstream movers and non-movers. Observed distances from recaptured individuals designated by star.

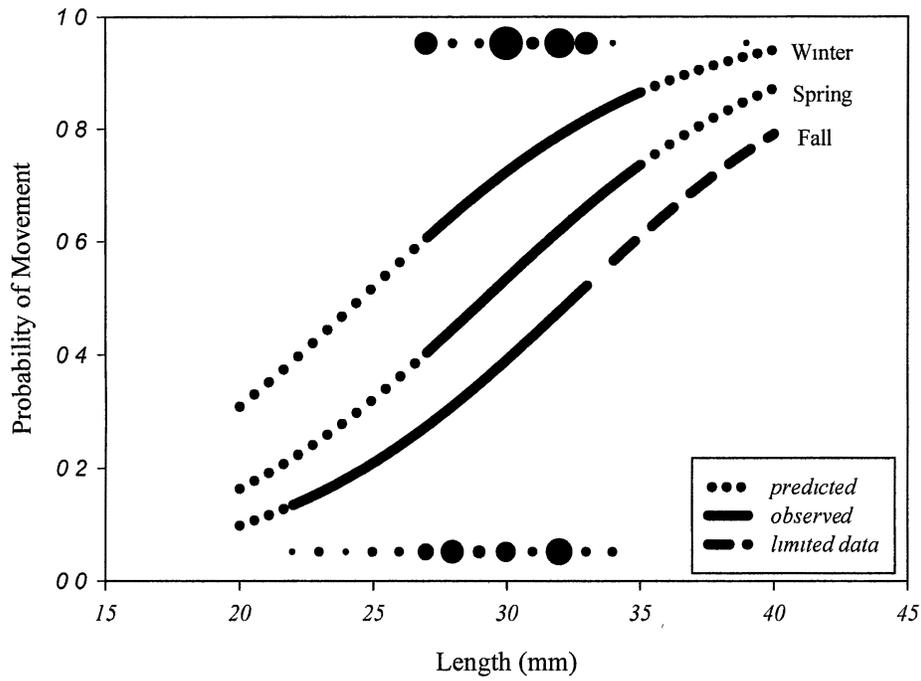


Fig. 7. Logistic regression model of the probability of fountain darters leaving the location of initial capture based on total length and season.

APPENDIX

POPULATION ESTIMATE OF *E. FONTICOLA* IN A 100-M REACH OF THE COMAL RIVER (OLD CHANNEL)

Objective: To estimate population size for 100 m river reach in the old channel of the Comal River, New Braunfels, Texas using mark-recapture techniques, as well as, document survival in a wild population of fountain darters.

Methods: A mark-recapture study was conducted in the old channel of the Comal River (see Methods: Chapter I). Information gathered on the number of fish captured, marked, and recaptured was used to estimate the total population size. The Schnabel method was used (Schnabel 1938), a modification of the Lincoln-Petersen model, as it can incorporate multiple recapture events into a single population estimate. The population estimate was only made for the first sampling period (August – October) to maximize the adherence to model assumptions such as a no immigration or births between captures, no emigration, no differential mortality between marked and unmarked individuals, and no marks are lost.

Results and Discussion: Estimated population size (95% CI) for fountain darters in the 100 m study reach was 2,732 (2,012 – 4,254) (Table A.1). Population estimate and confidence intervals are similar of those reported by Schenck & Whiteside (1976; 102,966 darters, no confidence interval given; approximately 2000 darters / 100 m) in the upper 5 km of the San Marcos River and by Linam et al. (1993; 168,078 darters, 114,187 - 254,110; approximately 2800 darters / 100 m) in 6 km of the Comal River system. However, caution should be used in comparing population estimates. Two different techniques for generating population estimates were used: mark and recapture (this study) and extrapolations of density data from available habitats (Schenck and Whiteside 1976; Linam et al. 1993). Also, amount of available habitats differed between the Linam et al. (1993) study and this study. Linam et al. (1993) estimated that filamentous algae

accounted for 33% of the total area of the old channel during their study period whereas a substantial proportion of this habitat had been displaced throughout the old channel prior to this study (personal observation).

Longevity

No information on the longevity of individual fountain darters has been documented in wild populations. Several individuals were recaptured in sampling subsequent to the conclusion of this study and a single individual was captured 19 months post-marking. Growth rate based on laboratory trials (Brandt et al. 1993) suggest that this individual was at least 22 months old. A few individuals reared and kept in laboratory studies have survived over 4 years (Brandt 1993). Maximum age documented for other species of the subgenus (*Microperca*) is over 1 year for the cypress darter (*E. proeliare*) (Burr & Page 1979) and up to 37 months for the least darter (*E. microperca*) (Johnson & Hatch 1991). Johnson & Hatch (1991) suggest that the longevity of the least darter combined with iteroparity provides a mechanism by which reproductive success in the species is less vulnerable to catastrophic disturbance events. The fountain darter spawns year round which combined with rapid sexual maturation, 6 months in laboratory trials (Brandt et al. 1993), and longevity of the species might provide a hedge against short term catastrophic disturbance events with respect to reproductive success.

Table A.1. Total number of fountain darters captured (C), cumulative number marked in population (M), and recaptured (R) during each sampling event of the summer-fall sampling period. As well as equations used to generate population estimate and confidence interval.

sample period	C	M	R	C * M
August	177	0	0	0
September	265	177	14	46905
October	82	428	16	35096
Σ			30	82001

$$\hat{N} = \frac{\sum_{t=1}^n (C_t * M_t)}{\sum_{t=1}^n R_t} \quad 95\% \text{ CI} = \frac{1}{\hat{N}} \pm 1.96 * \sqrt{\hat{V} * \left(\frac{1}{\hat{N}}\right)}$$

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