1	Barriers impede upstream spawning migration of flathead chub, a pelagic spawning
2	cyprinid
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24	Running Head: Flathead chub spawning migration

25 Abstract

26 Pelagic spawning cyprinids are declining throughout the North American Great Plains. 27 These species require long reaches of contiguous, flowing riverine habitat for drifting eggs and 28 larvae to develop, and their declining populations have been attributed to habitat fragmentation 29 or barriers (e.g., dams, dewatered channels, and reservoirs) that restrict fish movement. Upstream 30 dispersal is also needed to maintain their populations, and prior researchers have suggested that 31 members of this reproductive guild migrate upstream to spawn. To test this hypothesis, we 32 conducted a mark-recapture study of flathead chub *Platygobio gracilis* within a 91 km reach of 33 continuous riverine habitat in Fountain Creek, CO (USA). We measured catch per unit effort 34 (CPUE), spawning readiness (percent of flathead chub expressing milt), and fish movement 35 relative to a channel-spanning dam (Owens Hall Diversion Dam, OHDD). Multiple lines of 36 evidence indicate that flathead chub migrate upstream to spawn during summer. CPUE was 37 much higher at the base of the OHDD than at downstream sites, the seasonal increases in CPUE 38 at the OHDD closely tracked seasonal increases in spawning readiness, and marked fish moved 39 upstream as far as 33 km during the spawning run. The upstream migration was effectively 40 blocked by the OHDD. CPUE of flathead chub was much lower upstream of the OHDD when 41 compared to downstream sites and <0.2% of fish marked at the OHDD were recaptured 42 upstream. This study provides the first direct evidence of spawning migration for pelagic 43 spawning cyprinids and supports the general hypothesis that barriers to dispersal may disrupt the 44 source-sink dynamics necessary to maintain populations of flathead chub and other pelagic 45 spawning cyprinids.

46

47 Fishes depend upon unrestricted movement between various habitat types over their life-48 history (Schlosser and Angermeier 1995). Dams and diversion structures that restrict such 49 movement can be detrimental to migratory species, especially when spawning habitats are 50 isolated from downstream populations (Fullerton et al. 2010). Most prior work on the effects of 51 migration barriers has focused on commercially important diadromous species such as 52 salmonids, anguillids, and clupeids (Kemp and O'Hanley 2010), while barrier effects on small-53 bodied, potadromous fishes are poorly understood (Ficke and Myrick 2009). Streams of the 54 semiarid western U.S. and the Great Plains are highly fragmented by dams and other diversion 55 structures, and habitat fragmentation associated with these structures has been implicated in the 56 shrinking ranges and declining abundances of several plains fishes (Cross et al. 1985; Winston et al. 1991; Fausch and Bestgen 1997; Luttrell et al. 1999; Matthews and Marsh-Mathews 2007). 57 58 Consequently, improving and restoring the hydrologic connectivity of plains river systems has 59 become a cornerstone of plains fish conservation efforts (Fausch et al. 2002; Dodds et al. 2004; 60 Hoagstrom 2011, Perkin and Gido 2011). However, large-scale movements, particularly for 61 small-bodied plains species, remain poorly understood (Fausch et al. 2002).

One such species is flathead chub *Platygobio gracilis*, a plains river cyprinid that is 62 63 widely distributed from the Northwest Territory of Canada south to New Mexico, Texas, and 64 Louisiana (Lee et al. 1980). In spite of its vast distribution, extirpations throughout its range have 65 resulted in it being added to imperiled species lists in Colorado, Arkansas, Illinois, Kansas, 66 Kentucky, Mississippi, Missouri, Oklahoma, and Texas (Rahel and Thel 2004). In Colorado, 67 flathead chub occur mostly in plains portions of the Arkansas and the Rio Grande River basins 68 (Alves 1997; Nesler et al. 1999), where their range has shrunk based on historical records 69 (Woodling 1985). Barriers (e.g., dams, reservoirs, and dewatered channels) that limit dispersal

70	are thought to be a key factor in flathead chub declines in Colorado and elsewhere (Woodling
71	1985; Cross and Moss 1987; Pfliegler and Grace 1987; Bonner and Wilde 2000; Hoagstrum et al.
72	2007; Gido et al. 2010; Perkin and Gido 2011). Flathead chub occupy large, turbid river systems
73	(Rahel and Thel 2004) and are thought to belong to a guild of pelagic spawning cyprinids that
74	produce passively drifting eggs and larvae (Smith and Hubert 1989; Durham and Wilde 2006,
75	Durham and Wilde 2008; Perkin and Gido 2011). Pelagic spawners require long reaches of free
76	flowing habit for drifting eggs and larvae to develop, and river fragmentation leads to extirpation
77	of these species via reduced recruitment (Cross et al. 1985; Cross and Moss 1987; Pfliegler and
78	Grace 1987; Winston et al. 1991; Luttrell et al. 1999; Gido et al. 2010).
79	Upstream dispersal is presumed to be a critical mechanism by which pelagic spawning
80	cyprinids repopulate upstream reaches (Fausch and Bestgen 1997, Cross et al. 1985, Lutrell et al.
81	1999). These cyprinids are thought to migrate upstream to spawn (e.g., Cross et al. 1985;
82	Durham and Wilde 2008), where migrations serve to recolonize upstream reaches and to provide
83	adequate development time for drifting eggs and larvae (Durham and Wilde 2008). However,
84	support for this upstream spawning hypothesis is limited to indirect evidence (Rahel and Thel
85	2004). For example, Arkansas River shiner (Notropis girardi) are thought to migrate upstream to
86	spawn based on longitudinal distributions of adults (Durham and Wilde 2008) and drifting larvae
87	(Bonner 2000) during the spawning season. In addition, anecdotal evidence suggests that
88	flathead chub migrate upstream into tributaries to spawn in Wyoming streams (Rahel and Thel
89	2004). We have also observed large aggregations of flathead chub below dams in Colorado
90	during the summer spawning season (J. Bruce, unpublished data), suggesting an upstream
91	migration impeded by barriers.

92 These factors, combined with recent efforts in Colorado to improve fish passage in Plains 93 river networks, prompted a 2010 study to evaluate spawning related movement of flathead chub 94 in Fountain Creek, CO relative to a channel-spanning dam (Owens-Hall diversion dam, OHDD). 95 Our goal was to provide managers with information on flathead chub movement in order to 96 optimize the operation of a planned fish way for the OHDD. Our objectives were to determine 1) 97 if and when flathead chub migrate upstream to spawn 2); how far they move; and 3) if they are 98 able to pass the OHDD under its present configuration. We conducted a large-scale survey and 99 mark-recapture study of flathead chub up- and downstream of the OHDD to achieve these 100 objectives. We hypothesized that flathead chub migrate upstream to spawn and that this 101 migration is blocked by the OHDD. If so, we expect that flathead chub catch rate at the OHDD 102 will be higher than at downstream sites and that flathead chub catch rate at the OHDD will be 103 highest during the spawning season. Quantitative movement studies are lacking (Rahel and Thel 104 2004), so we did not develop a priori expectations regarding the distance that flathead chub 105 would move. Additionally, we hypothesized that the OHDD has low barrier passability. If so, we 106 expect that flathead chub catch rate would be greatly reduced upstream of OHDD and that few 107 fish marked downstream would be recaptured upstream of the dam.

108

Methods

Study area.- Fountain Creek is a large tributary (basin area 2,398 km²) of the Arkansas River in south-central Colorado (Figure 1). Basin elevation ranges from 1,432 m at the confluence with the Arkansas River to 4,300 m at the summit of Pikes Peak (Hansen and Crosby 1982). Channel form alternates between braided reaches and meandering, single-thread reaches. Wetted width is typically between 12 and 40 m within the study section. Streambed material is dominated by sand and small gravel with unstable large woody debris piles in the channel and

115	along the banks. Fountain Creek hydrology is strongly influenced by agricultural, urban, and
116	industrial water use and management (Stogner 2000; Edelmann et al. 2002). Average daily
117	stream discharge is 3.47 m^3 /s (range 1.84-14.19 m^3 /s), and average peak flow is 177.16 m^3 /s
118	(range 1.35-569.23m ³ /s; USGS gage 07106000, discontinuous period of record from 1941 to
119	2010, 39 years of complete record). The lower reaches of Fountain Creek (Figure 1) maintain
120	one of the last populations of flathead chub within the Arkansas River basin (Woodling et al.
121	1985). Flathead chub have been extirpated from the mainstem Arkansas River upstream of
122	Florence, CO and downstream of John Martin Reservoir (Las Animas, CO) in eastern Colorado
123	and Kansas (Woodling 1985, Gido et al. 2010, Perkin and Gido 2011).
124	Sample Sites We sampled 100 m reaches at 10 sites along 43 river kilometers (rkm) in
125	Fountain Creek near Fountain, CO (Figure 1). The study section is part of a larger 91 rkm
126	fragment of contiguous riverine habitat extending from the OHDD downstream into the
127	Arkansas River (Figure 1). One site was located at the base of the OHDD with eight additional
128	sites distributed downstream of the OHDD. In order to detect both smaller scale and larger scale
129	movements, distance was approximately doubled between sites downstream from the OHDD.
130	We also sampled at the base of the next upstream barrier from the OHDD (Chilcotte Diversion,
131	Site 0).
132	Fish sampling. – We sampled each site multiple times between April and October 2010
133	(Table 1) using backpack electrofishers (Smith-Root Model LR-24). We sampled in an upstream
134	direction along each stream bank without block nets for two complete passes. We used two

- electrofishers simultaneously followed by multiple netters in most cases, but occasionally a
- 136 single unit was used. Fish from each pass were held separately in 20-liter buckets and/or in-

stream live wells. All flathead chub were identified, enumerated, and measured (total length) tothe nearest millimeter in the field.

139 Fish marking and spawning readiness. – Flathead chub were batch marked 140 subcutaneously with site-specific color and body position combinations using elastic fluorescent 141 polymer (Northwest Marine Technology, Seattle, Washington, USA) and returned to the stream. 142 We only marked adult fish (\geq 80 mm TL based on age-length studies summarized by Rahel and 143 Thel 2004) as these are most likely to undertake spawning migrations. After the first sampling 144 event, we inspected all adult flathead chub for marks using long-wave ultraviolet light. Newly 145 encountered flathead chub were marked, and any recaptures were recorded and remarked if 146 previously captured at another site. We collected 21,245 flathead chub, of which 10,320 were 147 marked. We maintained 30 marked individuals in aquaria over the course of the study. Mark 148 retention for these fish was 100% with 0 mortalities.

We assessed spawning condition of adult flathead chub by applying light pressure to the abdomen and recording the presence/absence of milt. We used these data to calculate spawning readiness as the percent of flathead chub expressing milt. We used percent of total catch because flathead chub lack sexually dimorphic traits (Rahel and Thel 2004), and we could not reliably determine sex unless fish extruded gametes. We did not record data on extruded eggs or note gravid females since we could not consistently determine if swollen abdomens were related to ripe ovaries or full stomachs.

Data analysis. – We calculated catch per unit effort (CPUE; number of flathead chub/min
of electrofishing) using first pass data to control for differences among sites, sampling events,
and sampling time. We used analysis of variance (ANOVA) to determine if variability in mean
CPUE values was associated with site, and used Bonferroni-adjusted post-hoc tests to test for

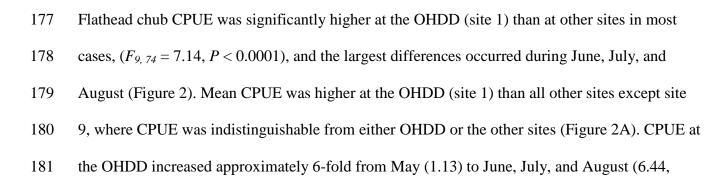
160 mean differences between sites ($P \le 0.05$). We used a student's t-test to determine if mean CPUE 161 at the OHDD was different from the remaining sites ($P \le 0.05$) during the summer spawning 162 months of June, July, and August. Data were pooled across the remaining sites because we were 163 unable to sample all sites multiple times per month and because preliminary analysis indicated 164 that CPUE at the OHDD was consistently much higher than all other sites during summer.

165 All remaining analyses relied on sample data combined from both passes. We compared 166 the percent of total flathead chub expressing milt at the OHDD (site 1) to all other sites, and data 167 were pooled as described above. We also calculated the distance and direction fish moved using 168 individual recapture data. Detailed analysis of the timing and directionality of fish movements is 169 beyond the scope of this paper, but is the subject of ongoing modeling efforts. Additionally, we 170 calculated barrier passability (the proportion of fish able to pass a barrier while migrating 171 upstream, O'Hanley and Tomberlin 2005) as the percent of fish marked at the OHDD that were 172 recaptured at the Chilcotte diversion dam (site 0, Figure 1). This assumes that all fish captured at 173 the OHDD intended to pass upstream of the dam and that these fish would move upstream 174 through the 9.7 km reach separating the two barriers.

175

Results

176 Spatial and temporal variation in flathead chub CPUE



182 6.71, and 5.60, respectively). In contrast, mean monthly CPUE was low and invariant (around

183 1.5) at the other sites until October when CPUE increased (3.92; Figure 2B). CPUE was around

4-fold higher at the OHDD than at other sites during June, July, and August ($t_{12.43} = 5.97, P < 10^{-10}$

185 0.0001; equal variances not assumed).

186 Temporal and spatial variation in spawning readiness

187 Temporal patterns in spawning readiness (the percent of male flathead chub expressing milt)

188 indicate that flathead chub spawn in summer (Figure 3). Spawning readiness was high from May

through August, and peaked in June and July. In contrast, few flathead chub (<3% of total catch)

190 expressed milt during April, September, and October. Spawning readiness in May was much

191 higher at the OHDD (mean 15.9%) than other sites (2.0%), but values were similar between the

192 OHDD and other sites during the remainder of the study (Figure 3).

193 Movement distance

194 We recaptured 741 fish (7.2 % of fish marked) and detected up- and down-stream movements

across the entire 33 km study section downstream of the OHDD (Figure 4). Most fish were

196 recaptured at the same site, and these were dominated by individuals marked at the OHDD.

197 Overall, nearly 82 % of marked fish were recaptured within 1 km of their initial marking site.

198 The remainder moved between 2 and 15 km except for 2 individuals that moved 33 km (one

199 upstream and one downstream).

200 Barrier passability of the Owens-Hall diversion dam

201 The OHDD blocked nearly all upstream movement of flathead chub. We marked or recaptured

202 6,032 fish at the OHDD structure during June, July, and August, but only 10 (0.17 %) were

recaptured 9.7 km upstream at the Chilcotte Diversion dam (Figure 1). Mean monthly total catch was more than an order of magnitude lower at the Chilcotte Diversion (15 ± 8 ; 1 SD) than at the OHDD (505 ± 168) during the peak spawning months of June, July, and August (Table 1).

206

Discussion

207 Extirpation of flathead chub and other pelagic spawning cyprinids is directly related to 208 habitat fragmentation (Gido et al. 2010; Perkin and Gido 2011). Recruitment bottlenecks 209 associated with drifting eggs and larvae are a key factor in these extirpations (Platania and 210 Altenbach 1998; Dudley and Platania 2007), but upstream movement of juveniles and or adults 211 must play an important, yet unproven, role in maintaining populations (Fausch and Bestgen1997; 212 Luttrell et al. 1999). Testing this upstream movement hypothesis is challenging due to the 213 logistical constraints of detecting small-bodied fish movements in large riverine habitats, but 214 here we found strong support for the hypothesis that flathead chub migrate upstream to spawn. 215 Catch rates were highest at the upstream barrier and tracked seasonal differences in male 216 spawning readiness. We also measured movements of at least 33 rkm during the spawning 217 season. To our knowledge, these findings are the first direct evidence of large-scale movements 218 (10s of km) of North American adult pelagic spawning cyprinids. 219 Plains fishes thrive in harsh stream environments that are prone to drying, flash floods, and 220 poor water quality (Matthews 1985; Fausch and Bestgen 1997; Dodds et al. 2004). 221 Paradoxically, many of these tolerant species are increasingly in need of conservation efforts due 222 to declining populations (Fausch and Bestgen 1997; Hoagstrum et al. 2011). Pelagic spawning 223 minnows in particular suffer high rates of imperilment (Jelks et al. 2008) and are being 224 systematically extirpated throughout the Great Plains (Fausch and Bestgen 1997; Gido et al. 225 2010; Perkin and Gido 2011). The case of the flathead chub epitomizes the declines seen across

226 this reproductive guild of fishes. Formerly common and abundant over a vast area stretching 227 from Northern Canada to Louisiana, they are now extirpated from large parts of their range 228 (Woodling 1985; Cross and Moss 1987; Pfliegler and Grace 1987; Bonner and Wilde 2000; 229 Hoagstrum et al. 2007; Gido et al. 2010) including most (61%) of the large stream fragments 230 remaining in the Great Plains portion of the U.S. (Perkin and Gido 2011). Efforts to identify 231 mechanisms of extirpation in pelagic spawning minnows have coalesced around two critical 232 factors: 1) movement at multiple life stages is an important life history strategy for this guild 233 and, 2) barriers restrict these movements, disrupting the source-sink dynamics necessary to 234 maintain populations (Cross and Moss 1987; Winston et al. 1991; Fausch and Bestgen 1997; 235 Platania and Altenbach 1998; Luttrell et al. 1999; Bonner and Wilde 2000; Gido et al. 2010). Our 236 key findings that 1) adults migrated upstream to spawn and 2) their migration was effectively 237 blocked by a dam support this general model of species decline. Likewise, these findings support 238 calls to preserve large reaches of riverine habitat and to reconnect fragmented segments as a 239 general strategy for conserving populations of flathead chub and other pelagic spawning 240 cyprinids (Fausch and Bestgen 1997; Fullerton et al. 2010; Hoagstrum et al. 201; Perkin and 241 Gido 2011).

The lower reaches of Fountain Creek support a large population of flathead chub (we marked >10,000 adults) even though it is part of a stream fragment that is only 91 rkm long. This is considerably shorter that the predicted minimum length of riverine habitat needed to sustain populations of flathead chub and other pelagic spawning cyprinids. Perkin and Gido (2011) modeled occurrences of 8 pelagic spawners in large stream fragments of the U.S. Great Plains and estimated that 183 rkm was the minimum fragment length for persistence of flathead chub and that all species suffered 100% extirpation in fragments <103 rkm. It is possible that flathead

249 chub persist within this fragment because flowing water is maintained in the channel throughout 250 the spawning season. Perkin and Gido (2011) noted that extirpations of pelagic spawning 251 minnows occurred to the greatest extent in the south and central Great Plains where water 252 withdrawals cause extensive stream drying during the summer spawning season. Stream 253 discharge in Fountain Creek downstream of Colorado Springs is heavily augmented by treated 254 wastewater effluent, and median daily stream discharge during spawning season (mid-May through August) typically range between $0.27 - 2.24 \text{m}^3/\text{s}$ near its confluence with the Arkansas 255 256 River (U.S. Geological Survey gage 07106500, discontinuous period of record from 1922 to 257 2010, 68 years of complete record).

258 Implications for management of the OHDD

259 The OHDD limits access of flathead chub to upstream reaches as it is currently operated. 260 Catch rate and abundance were much lower upstream of the OHDD, and passability of the 261 OHDD was low. Less than 0.2% of flathead marked at the OHDD were recaptured upstream. 262 Approximately 6.0 % (10) of the adult fish captured at the Chilcotte Diversion (site 0; Table 1) 263 were originally marked downstream of the OHDD structure (site 1). It is unclear if the remaining 264 94% (170) were resident fish between the two diversion structures or if fish captured at the 265 Chilcotte Diversion had successfully passed the OHDD in 2010. We observed flathead chub 266 repeatedly and unsuccessfully attempt to swim up the thin sheet of water spilling over the face of 267 OHDD, suggesting that individuals would have continued upstream were their progress not 268 impeded by the dam. The OHDD has a head gate that is opened periodically (mostly weekly) to 269 flush accumulated sediments, and it is possible that flathead chub pass the barrier during these 270 operations.

271 Plans are underway to install a fishway to improve passage of the OHDD. This fishway 272 should be operated to maintain optimal flows for flathead chub passage in June, July, and August 273 during the peak of the spawning run. If possible, fishway operations should be extended into 274 May and September to accommodate early and late spawners. Spawning readiness (proportion of 275 flathead chub expressing milt) was higher at the OHDD than downstream in May, suggesting an 276 early onset of the spawning run. Likewise, catch rates remained high at the OHDD into 277 September, even though we had inadequate temporal replication at the site to precisely determine 278 the end of spawning run.

279 Improving passage of the OHDD is a sensible first step for conserving this remnant 280 population of flathead chub. The OHDD is the lowest barrier on Fountain Creek (Figure 1) and 281 intercepts fish from 10s of km downstream (Figure 1). We suspect that flathead chub migrate 282 into Fountain Creek from the mainstream Arkansas River during spawning season, and 283 additional mark-recapture studies are underway to address this possibility. If flathead chubs 284 could move upstream of the OHDD to the Chilcotte Diversion, this would extend the reach an 285 additional 10 km to 101 km, close to the minimum fragment length associated with persistence 286 of pelagic spawning minnows (Perkin and Gido 2011). Upstream of the Chilcotte Diversion, 287 Fountain Creek is highly fragmented with 29 potential barriers (diversion dams and grade control 288 structures) located over the next 40 rkm. Considering the high degree of fragmentation in these 289 upstream reaches, the greatest near-term ecological benefits for flathead chub will likely be 290 gained by increasing passability of the downstream-most barriers in Fountain Creek.

291

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Table 1. Monthly total number of flathead chub \geq 80 mm captured at each site using two-pass electrofishing, Fountain Creek, 2010. Standard deviation is in parenthesis followed by the number of samples collected that month. Total numbers without standard deviation were visited < three times and totals without an indicated number of samples were visited once. ---- indicates site was not visited during that month.

Site	Apr	May	Jun	Jul	Aug	Sept	Oct
0			25, (13), 3	58, (10), 4	70, (21), 3	27, 2	
1		148, (38), 3	2105, (301), 4	3306, (384), 5	980, (174), 3	191	114
2		54, 2	239, (119), 3	44	3	351	
3		33	214, 2	128	28	39	
4		123, 2	72, 2	22	16	32	
5	54	63	168, 2	219	27		293
6	130, 2	71	358, 2	172	22	67	181
7	353, 2	193	326, 2	98	76		62
8		89	107, 2	10	131	67	
9		201, 2	604, 2	162	106		247

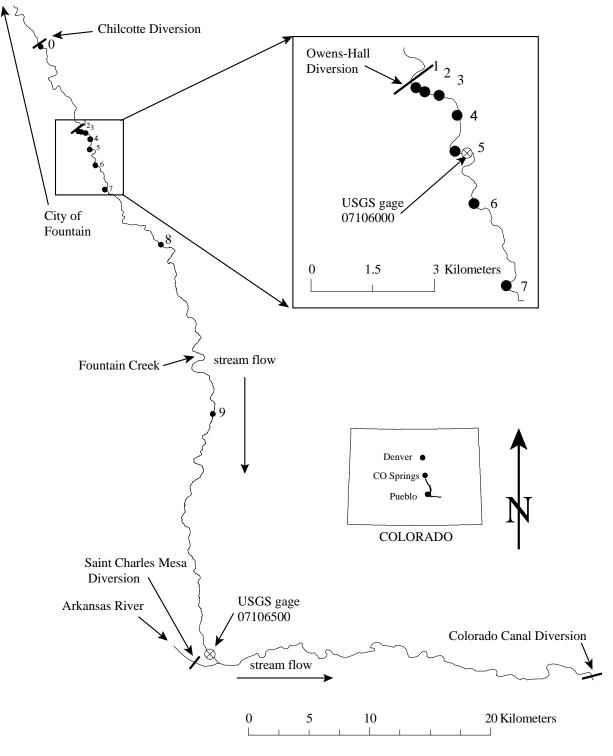


Figure 1. Study area showing approximate locations and distance between 10 sampling locations and upstream dispersal barriers (diversion structures) within the study reach. Numbers next to site locations (closed circles) are site numbers in Table 1.

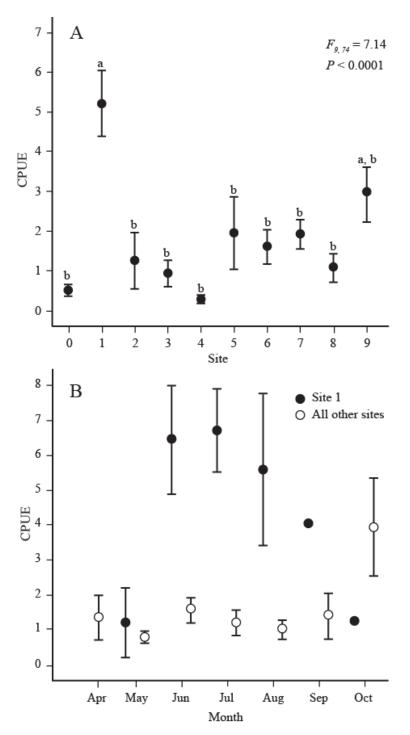


Figure 2. Mean (\pm SE) catch per unit effort (CPUE; number of flathead chub/min of electrofishing) of flathead chub at each site between April and October (A) and at site 1 relative to all other sites for each month (B), Fountain Creek, 2010. Letters indicate significant differences ($P \le 0.05$, Bonferroni adjusted).

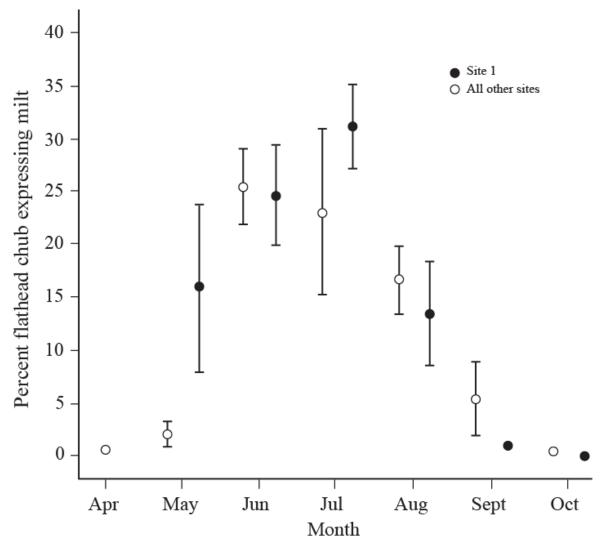


Figure 3. Percent (± SE) of adult flathead chub (\geq 80 mm) captured from Fountain Creek expressing milt between April and October, 2010 at site 1 and at all remaining sites.

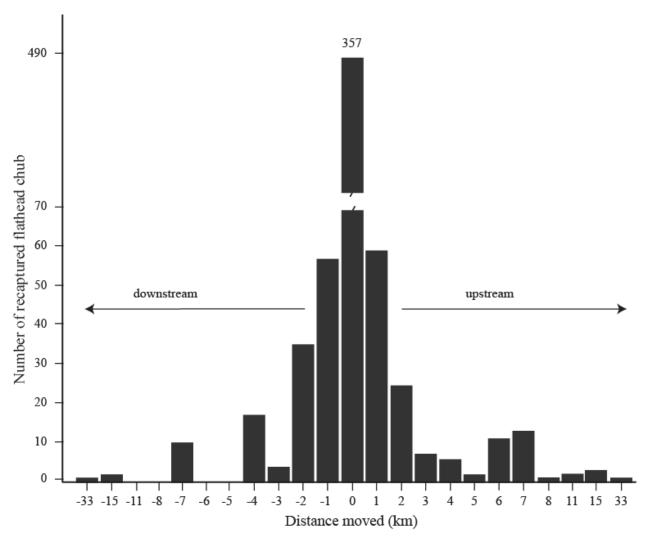


Figure 4. Number of recaptured flathead chub \geq 80 mm and the upstream and downstream distances moved from where they were origianly marked, Fountain Creek, April to October, 2010. Number above the zero bar indicates the number of flathead chub that were marked and recaptured at the Ownes-Hall Diversion structure (Site 1).