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Abstract

This study characterized spatial and temporal patterns associated with riverine broadcast spawning pygmy whitefish (*Prosopium coulterii*) in tributaries of Chester Morse Lake (CML), near Seattle, Washington, from 2001 to 2012. In most years, fish spawned in a narrow linear reach of riverine habitat from 2.0 to 3.0 km upstream of CML within a two week period. Individual characteristics of spawning pygmy whitefish were investigated through the use of mark-recapture efforts and a PIT (passive integrated transponder) tag antenna array. During the latter years of the study (2006–2011), a total of 3,012 fish were captured and PIT tagged. Returning female pygmy whitefish spent less time in the river (mean 2.4 days, SD 3.1) than males (mean 5.9 days, SD 2.4). In addition, 91% of all movements occurred between 1700 and 0700 during nighttime hours suggesting that spawning pygmy whitefish are most active under the cover of darkness. Thirteen fish returned for a fifth spawning migration and one individual was detected six years after initial tagging, demonstrating that pygmy whitefish spawn in multiple years and that fish can live to at least age nine in the CML population. These data represent the first attempt to investigate return frequency and other reproductive characteristics of riverine spawning pygmy whitefish throughout their range, and supports the development of practical management techniques for this and similar riverine broadcast spawning species.

Keywords: pygmy whitefish, spawning, broadcast, residence time

Introduction

Broadcast spawning fish are found in a wide range of habitat types from ocean reefs, to lakes and ponds, or rivers and smaller streams. This spawning behavior does not require the large energetic investment involved in excavating redds incurred by many other riverine salmonid species. Another advantage of broadcast spawning is that eggs are distributed across a broader spatial area and drift to incubation sites, reducing the concentration of eggs at any specific location. However, eggs spawned in this fashion may be vulnerable to environmental disturbances such as scouring flows, seasonal drying in stream systems (Wilde and Durham 2008), or changes in water elevation during incubation. Broadcast spawning in riverine habitat is a strategy used by a limited number of stream breeding fish species in the western United States (Beauchamp 1990; Parsley et al. 1993). Although it may not be common, broadcast spawning fish are often a key forage base supporting larger predatory species (e.g., Connor et al. 2001).

The pygmy whitefish (Prosopium coulterii) is a broadcast spawning species that inhabits the lower depths of cold water lakes and typically persists in relatively oligotrophic systems (Hallock and Mongillo 1998, Wydowski and Whitney 2003, Zemlak and McPhail 2006). Pygmy whitefish were long thought to be a North American endemic species; however, in the 1990s the species was discovered in three lakes in the Amguem River system in the Chukotsk Peninsula, Siberia (Chereshnev and Skopets 1992). In North America, pygmy whitefish are widely distributed west of the Continental Divide but are uncommon east of the Divide (McPhail 2007). Populations are patchily distributed, found in Lake Superior, as well as in lakes in Washington, Idaho, Montana, Alaska, and western Canada (Witt et al. 2011).

Overall, very few details of spawning ecology, timing, and location are available for the species. Riverine broadcast spawning is common in several populations where schools of pygmy whitefish congregate at river mouths to spawn

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(Fraley and Shepard 1989, Hallock and Mongillo 1998, Wydowski and Whitney 2003). Early winter spawning has been reported for pygmy whitefish in Lake Superior (Eschmeyer and Bailey 1955) and in Alaska (Heard and Hartman 1966) as evidenced by samples containing gravid females. During this period of the year, precipitation falls primarily as snow and spawning during this time may offer protection against higher streamflow as well as more predictable flow conditions in portions of the species range. At northern latitudes, females approaching ovulation were captured in a central British Columbia lake in October, shortly before the lakes froze over (McPhail and Zemlak 2001), again suggesting that the onset of winter weather conditions plays a role in spawn timing.

Effective management of habitat diversity for pygmy whitefish requires the maintenance of stream networks (Taylor et al. 2011). However, little information is available regarding specific spawning or incubation sites, physical characteristics of spawning individuals, or the frequency of spawning. Basic reproductive information about pygmy whitefish is needed to fill the existing void and to provide a basis for identifying spawning habitat or to develop monitoring techniques for assessing spawning populations.

We evaluated the spatial and temporal patterns of a riverine spawning pygmy whitefish population over multiple years in the Chester Morse Lake (CML) basin. Specific objectives for the study included (1) determining the spatial distribution of pygmy whitefish spawning schools relative to the lake; (2) determining the initiation and temporal distribution of spawning among years; and (3) describing population characteristics of the spawning run through mark-recapture efforts (sex ratios in spawning schools, mean fork length at spawning, number of spawning events for an individual, and degree of site fidelity). These data provide useful information to predict the habitat used for spawning and to assist management and conservation efforts for the species throughout its range.

Study Area

The Cedar River Municipal Watershed (CRMW) is owned by the City of Seattle and managed to supply drinking water, instream flows for fish, and a small amount of hydroelectric power, as well as to maintain and restore natural ecosystem processes (City of Seattle 2000). Chester Morse Lake, the watershed's main reservoir, is located inside the CRMW, and was formerly a natural lake (Cedar Lake) with an elevation of 467.1 m (above mean sea level). The main basin of the reservoir is steeply sloped dropping to a depth of 35 meters in the center of the lake. A thermocline develops at approximately 10-15 m in July, but water temperatures at the bottom of CML remain cold throughout the year (< 8.0 °C) (SPU unpublished data).

Four fish species are present in the lake and its tributaries including native bull trout (*Salvelinus confluentus*), pygmy whitefish, shorthead sculpin (*Cottus confuses*), and introduced rainbow trout (*Oncorhynchus mykiss*). Pygmy whitefish provide an important food resource for adfluvial bull trout in CML, a species listed as threatened under the Endangered Species Act, especially during spring months (Connor et al. 2001). Colonization of CML by anadromous or migratory fish is blocked by a natural falls barrier downstream of the Masonry Dam on CML, thereby isolating these populations since glacial times.

Two main tributaries flow into CML from the crest of the Cascade Mountain range and provide low gradient (< 1%) habitat where pygmy whitefish schools are observed each winter immediately upstream of CML. Approximately 24 km of linear stream habitat is available on the Cedar River and 6 km is available on the Rex River (Figure 1). The mainstem habitat of both river systems contains low gradient reaches, averaging less than 1.0% gradient for approximately the nearest 2.0 km upstream of CML (Cedar average wetted width ~ 20 m, Rex average wetted width ~ 15 m). The gradient of other smaller tributaries feeding directly into CML increases steeply from the lake confluence (> 5.0 % gradient) and pygmy whitefish have not been observed in any of these streams.

Methods

Spawning Surveys

Habitat was visually surveyed for the presence of pygmy whitefish schools in several reaches of the

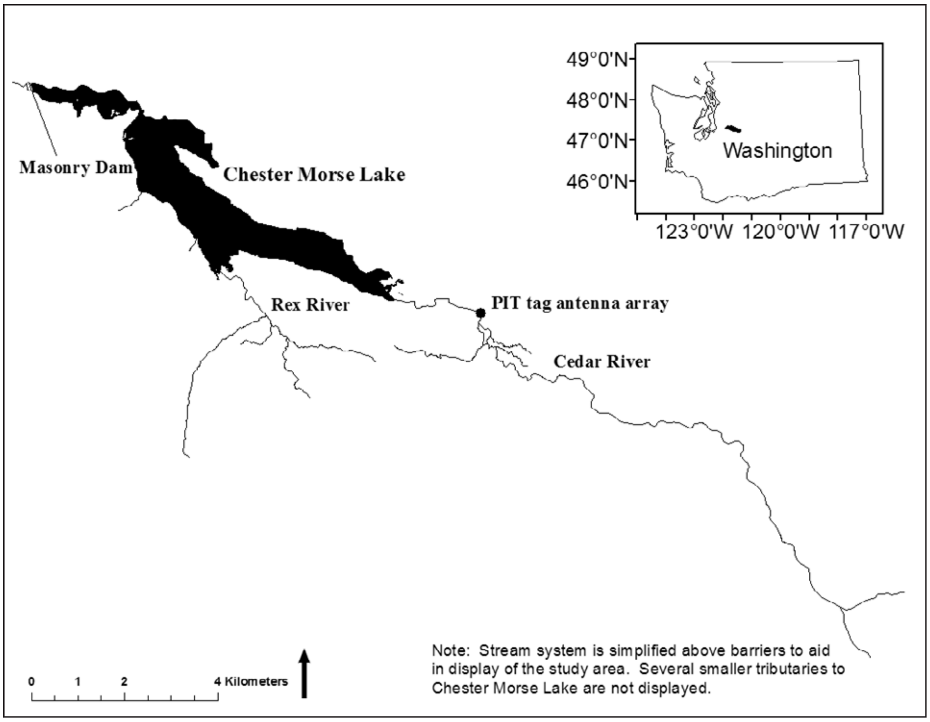

Figure 1. Location of the Cedar and Rex Rivers upstream of Chester Morse Lake used by pygmy whitefish for spawning in the upper Cedar River Municipal Watershed.

Cedar and Rex Rivers upstream of CML from 2001 to 2011. As pygmy whitefish were known to use the same spawning reaches as bull trout (Connor et al. 2001), surveys occurred concurrently during bull trout spawning surveys initiated in late September (Barnett et al. 2013), and continued through December, so that the beginning and end points for pygmy whitefish spawning were captured annually. Past research indicated that pygmy whitefish spawn in tributaries of CML after the majority of bull trout spawning was complete each year (Connor et al. 2001). Two surveyors walked the river from the lake mouth to approximately 4.0 km upstream of CML and recorded the location of each pygmy whitefish school (GPS point), visually estimated the number of individual fish in each school, and documented notes on behavior and habitat where fish were observed. The spatial and temporal distribution of pygmy whitefish was evaluated only for the Cedar River by creating box-and-whisker plots to display the median and range of school locations upstream of CML by year because so few pygmy whitefish were observed on the Rex River throughout the study.

Reaches of the Cedar and Rex Rivers where pygmy whitefish spawned were surveyed at least twice weekly, when stream flow and road access conditions permitted, to document changes in the spatial distribution and numerical counts of schools/individuals through the spawning run. The same group of experienced observers conducted all surveys, which aided in ensuring consistent results over the study (Muhlfeld et al. 2006, Howell and Sankovich 2012).

Fish Capture and Tagging

During spawning seasons 2006–2011, pygmy whitefish were captured from the Cedar and Rex Rivers by beach seining. Capture dates were spread throughout the run to ensure detection of variation in run timing between sexes. Although, temporal and spatial spawning characteristics were assessed only on the Cedar River, pygmy whitefish were tagged in both river systems to assess movement between tributaries of CML. Approximately

85–90% of PIT tags were inserted in fish in the Cedar River annually, with the remainder going to pygmy whitefish in the Rex River.

At each tagging site, a random sample of fish (100–150 fish) was transferred into net-pens in gently flowing water where they were held before handling. If more fish were captured in seine nets than could be tagged in a session, the remaining fish were tallied by sex and returned to the river. All fish were in reproductive condition when handled, so a sex determination was easily assessed on all individuals based on the presence of eggs or milt. These tallies provided the basis for determining the sex ratio of females to males for each spawning school. Several large schools were captured in 2007 and 2008 in an attempt to selectively tag female pygmy whitefish. Consequently, sex ratios based solely on the tagging numbers in those years suggest that females were more abundant than expected from sex ratio results obtained at the school level.

A 100 g/L solution of tricaine methanesulfonate (MS-222) was used to anesthetize pygmy whitefish before measurement and tagging with 12-mm PIT tags. Each fish was categorized by sex, measured (fork length [L_F] to nearest mm), and weighed (to the nearest 0.01g) before a PIT tag (12 mm, 0.09 g in air, 134.2 kHz; Biomark, Boise, ID) was inserted in the body cavity with a 12-gauge hand-held hypodermic needle with a sharp beveled edge. All sampled fish were left to recover in large totes stationed at the streamside (10–15 min) where water was frequently refreshed during recovery before release at the site of capture. All PIT tagging procedures followed the established guidelines outlined by the Columbia Basin Fish and Wildlife Authority (1999). The same tagging crew was used in all years of the study to minimize potential variation in survival due to handling and tagging effects on fish (Dare 2003).

PIT Tag Antenna Array

A PIT tag antenna array was installed on the Cedar River approximately 1.9 km upstream of CML in August 2005 as part of a study investigating outmigration of juvenile bull trout and rainbow trout. The array consisted of six 6 × 1 m rectangular antennas positioned in three rows and secured to the streambed (details provided in Mesa et al. 2008). Detections of unique PIT tags were recorded and stored to a full-duplex multiplexing transceiver (FS-2001M, Biomark, Boise, ID) stationed at the streambank. A PIT tag antenna array was not installed on the Rex River.

Temperature Monitoring

Continuous stream temperature and flow measurements were collected at a real-time USGS gage (12115000) located on the Cedar River 2.0 km upstream of CML, and daily averages are presented to compare the relationship between temperature, flow, and pygmy whitefish temporal spawning.

Data Analysis

An ANOVA was used to compare differences in fork length of tagged pygmy whitefish by sex. Instantaneous growth rate (G) of fish recaptured in multiple years was estimated with the following equation: $G = (\ln L_{F2} - \ln L_{F1})\,(t_2 - t_1)^{-1}$, where L_F represents fork length (mm) and t represents time (days) between capture events (Ricker 1975).

Detections at the PIT tag antenna array allowed us to examine the proportion of individuals returning to spawn one year post-tagging. The number of returning individuals in the year immediately after tagging was divided by the total number of fish tagged in that year. In addition, all PIT tag detections were classified as upstream or downstream movements by examining the pattern of detections across the antenna array. These movements were plotted by hour of the day to determine timing of movement over a 24-hour period. A chi-square goodness-of-fit test compared the distribution of timing of upstream movements to an expected distribution to examine diel patterns of movement. The number of days spent in the river for individuals detected entering and exiting the PIT tag antenna array was determined by subtracting entry date from exit date. Next, the mean number of days (± SD) spent in the river was calculated for males and females to determine residence time by sex. An ANOVA analysis compared differences in the mean number of days spent in river by year (for males) and by sex.

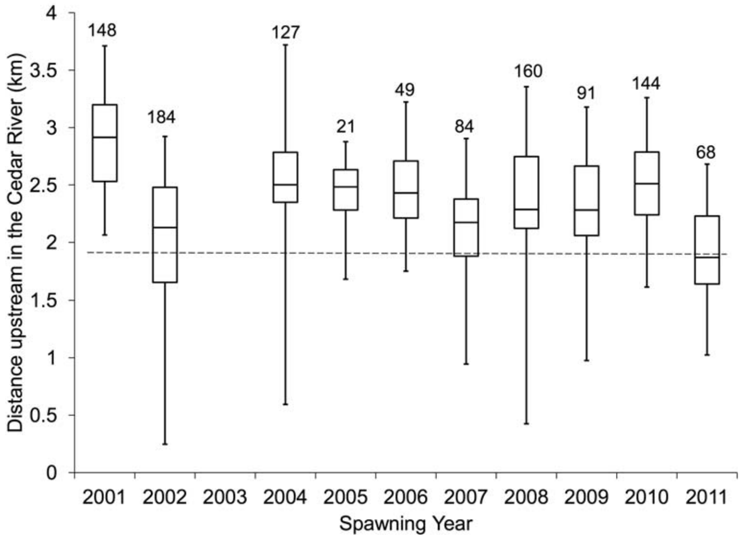

Figure 2. Distribution of pygmy whitefish schools for spawning years 2001–2011, in the Cedar River relative to Chester Morse Lake (horizontal line in box = median; ends of the box = 25th and 75th percentile; end of whisker = 10th and 90th percentile, sample size above each box). The dashed line at 1.9 km represents the location of a stationary PIT tag antenna array on the Cedar River.

Results

Spatial and Temporal Distribution

Schools of pygmy whitefish were distributed throughout the lowermost reaches up to 3.7 km upstream of CML in the Cedar River (Figure 2). Pygmy whitefish were observed in much lower density on the Rex River. Though this did not allow for meaningful comparison in timing, they were observed using habitat up to 2.3 km upstream of CML. In addition, no pygmy whitefish schools were observed in small floodplain channels or sidechannels of either the Cedar or Rex River system in any years despite biweekly surveys. Pygmy whitefish schools were observed primarily in glide or pool habitat types, but were also observed moving upstream through shallow riffle habitat and school size ranged up to an estimated 2,000 individual fish. Despite attempts to locate eggs, no spawning events were observed (evidenced by eggs) during surveys.

On the Cedar River, the median distance upstream of CML for pygmy whitefish schools in all years ranged from 1.9 to 3.0 km. Schools were not widely distributed in the river, and in fact, 50% of all pygmy whitefish school locations were located within 350 to 800 m of one another in any given year. The maximum distance a pygmy whitefish school was located upstream of CML was 3.7 km, which occurred in both 2001 and 2004.

The temporal distribution of the pygmy whitefish spawning run in the Cedar River ranged from 9 to 21 days (Table 1). Spawning schools were detected during the last week of November or the first week of December each year, and were observed for an average (SD) of 11.8 (4.1) days. During this time, average stream temperatures were cold (annual average of 2.7 to 5.1 °C) and streamflow was generally less than 8.5 cms.

Physical Characteristics of Tagged Pygmy Whitefish

Fork lengths of male pygmy whitefish varied over a relatively narrow range of 146.0 to 215.0 mm (n = 2,678), except for one male that was substantially smaller (L_F = 124.0 mm). Males had a pooled mean L_F (SD) of 180.4 mm (9.2). Females were significantly larger than males, with a pooled mean L_F (SD) of 196.5 mm (9.8), (range 170.0 to 238.0 mm), (t-test: t = 2.0, P < 0.001).

Annual growth values were calculated from 23 male pygmy whitefish recaptured during tagging

TABLE 1. The temporal distribution of riverine broadcast spawning pygmy whitefish, average river temperature (°C), and range of flow (cms) in the Cedar River, Washington, 2001–2012.

Spawning Year	Dates fish present (m/d)	Number days observed spawning	Average river temperature during run (°C)	Range of flow conditions (average daily cms)
2001	12/3–12/12	9	3.8	3.8–5.5
2002	12/13–12/23	10	4.2	2.6–5.9
2003	12/8–12/17 [a]	9	3.8	4.9–7.6
2004	11/22–12/1	9	5.1	3.4–30.3
2005	12/1–12/9	8	3.2	2.5–3.7
2006	12/4–n/a [b]	n/a [b]	3.6	4.1–4.6
2007	12/8–12/20	12	3.1	4.0–8.9
2008	12/1–12/16	15	4.0	4.8–7.3
2009	11/30–12/14	15	2.7	3.2–0.5
2010	11/29–12/9	10	3.7	3.0–6.3
2011	11/26–12/17	21	3.4	2.8–10.8
2012	11/26–12/13[c]	17	4.7	5.5–17.0

[a]Surveys were limited during 2003 due to a major windstorm, although we could not estimate numbers of fish, we are confident we captured the beginning and end of the run.

[b]Snow accumulation on the roads limited our access to the river during 2006 and we were unable to capture the end of the spawning run.

[c] PIT tag detections only, no spawning surveys conducted.

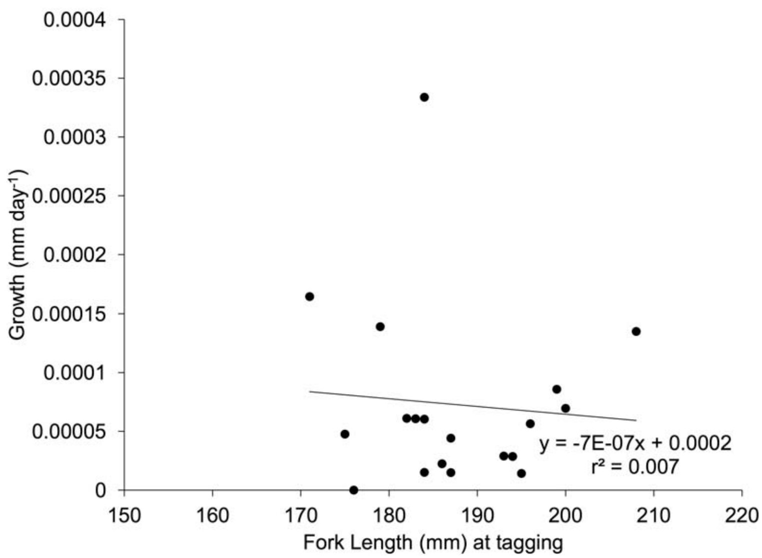

Figure 3. Instantaneous growth rate of male pygmy whitefish captured > 1 year post-tagging in the Cedar and Rex Rivers.

efforts in subsequent years (0.9% of total males tagged), but no females were physically recaptured during the study. No relationship was found between fork length at tagging and instantaneous growth (Figure 3, $r^2 = 0.007$). The absolute growth as expressed by increase in L_F (mm/year) ranged from 1.0 to 21.1 mm/year, averaging 4.9 mm/year. The largest increase in L_F was observed in a

TABLE 2. Sex ratios of pygmy whitefish collected from spawning schools in the Cedar and Rex Rivers (combined) by year, 2007–2010.

Year	Number of fish	Percent Female	Percent Male	Number of Schools
2007	1,803	9.6	90.4	9
2008	1,596	3.2	96.8	12
2009	966	3.1	96.9	5
2010	678	5.8	94.2	5

fish originally PIT tagged at 163.0 mm that grew to 184.0 mm the following year. Most pygmy whitefish grew 1.0 to 4.0 mm per year and in many cases was within the margin of expected measurement error (1.0–2.0 mm).

Sex Ratios of Spawning Schools

The sex ratio of spawning schools was determined by seining 5–12 large schools (> 100 fish per school) periodically while pygmy whitefish were present in rivers during four separate years (Table 2). The percentage of females captured was low in all years and varied from 3.1 (2008) to 9.6 (2007). The sex ratio in spawning schools was significantly different (ANOVA: $F_{1,\,60}$ = 7,885.2, $P < 0.001$), where males overwhelmingly dominated the capture.

Movement by PIT Tagged Fish

Individually tagged pygmy whitefish remained in the Cedar River system between 0.3 to 12.0 days. Although sample size was small for returning females (n = 19, all years pooled), a significant difference was determined between time spent in the river by females versus male pygmy whitefish. Males spent significantly more time in the river during the spawning run (median = 5.9 days; mean = 5.9 days, SD 2.4) than females (median = 0.8 days; mean = 2.4 days, SD 3.1 SD) (ANOVA: $F_{1,\,631}$ = 3.9, $P < 0.001$).

Most pygmy whitefish (91%) moved upstream over the PIT tag array during nighttime (sunset occurred at 1615 and sunrise at 0745) between 1700 to 0700 hours on the Cedar River (Figure 4). In addition, 94% of females moved upstream during these same nighttime hours. A chi-square goodness-of-fit-test indicated a significant difference in the distribution of movement timing for upstream moving fish (χ^2 = 1,027.4, df = 23, P < 0.001). Pygmy whitefish moved past the PIT tag array during daylight hours, but in much lower numbers than during nighttime hours.

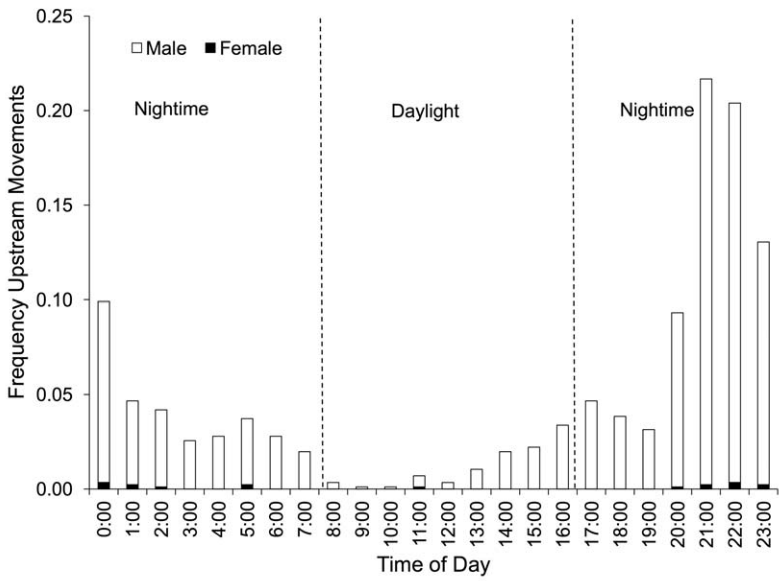

Figure 4. Time of upstream pygmy whitefish movements observed at the Cedar River PIT tag antenna array, 2007–2011 combined. Dashed lines represent average times for sunrise (0745) and sunset (1620) during the spawning season.

TABLE 3. Number of tagged pygmy whitefish by sex and the mean fork length (L_F) (± SD) at tagging in the Cedar and Rex Rivers combined, 2006–2011.

Tag Year	Number PIT Male	Tagged Female	Mean L_F (SD) Male	Mean L_F (SD) Female
2006	344	80	190.0 (12.7)	193.0 (9.9)
2007	341	145	186.4 (7.4)	196.1 (9.5)
2008	524	56	180.4 (9.8)	203.4 (10.4)
2009	476	23	179.1 (8.7)	195.3 (8.0)
2010	478	45	178.5 (8.8)	196.0 (6.7)
2011	499	1	175.6 (7.6)	181.0
Totals	2,662	350	179.6 (9.2)	196.4 (9.9)

Return of PIT Tagged Fish

The percentage of tagged individuals detected at the PIT tag antenna array one year post-tagging varied widely from 8.0% (returning 2010 tagged fish) to 49.9% (returning 2009 tagged fish) (Table 3, Figure 5). A low return rate was observed in 2011 (8.0%) and in 2012 (19.8%), but in all other years, more than 23.3% of tagged pygmy whitefish returned one year post-tagging. The percent of males returning one year post-tagging was significantly higher than females in all years (t-test: $t = 2.23$, $df = 8$, $P = 0.002$). Over seven years, an average 28.8% of males tagged were detected in subsequent years, while an average of only 3.7% of females returned in multiple years. The percentage of returning males reached a maximum for fish tagged, when 52.1% of all tagged individuals were detected in 2010.

Most pygmy whitefish detected in years after tagging were observed in consecutive years; however, several pygmy whitefish (n = 55) that returned in multiple spawning seasons skipped at least one year between detections. Movement between river systems showed that 12.6% of the individuals tagged in the Rex River (n = 34) moved to the Cedar River in the year after tagging. Although a PIT tag array was not installed on the Rex River, physical recapture of fish during tagging allowed the opportunity to document fish originally tagged in the Cedar River (n = 3) that had moved to the Rex River.

Pygmy whitefish originally tagged in 2006 (n = 424) had the opportunity to return in six additional spawning seasons. Most tagged fish were age four according to scale analysis (SPU unpublished data), and one male tagged in 2006 returned in 2011. This record suggests that the

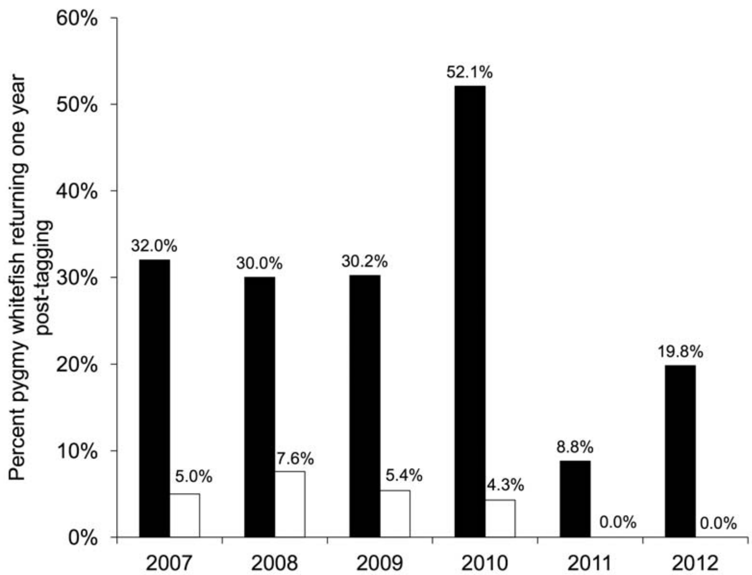

Figure 5. Percent of tagged male (solid black bars) and female (open bars) pygmy whitefish detected one year post-tagging at a PIT tag antenna array on the Cedar River, 2007–2012.

possible upper limit of life expectancy (at least for males) in this population is nine years. The likelihood of returning after being tagged, even in one additional year, was relatively low at only 16.0%. The curve for fish returning in consecutive spawning seasons slowly declined until the seventh spawning season when no individuals were detected.

Discussion

The results of this study provide the first detailed records characterizing temporal and spatial distribution of a riverine spawning population of pygmy whitefish in the species range, and demonstrate that fish return in multiple spawning seasons. Results from multi-year spawning survey efforts confirmed that the spawning run spans a short temporal period and occurs within a narrow spatial range immediately upstream of the lake. Tagging of individual fish allowed an assessment of individual's return frequency post-tagging and an evaluation of spawning residence time for females and males. Notably, the highly skewed sex ratio of spawning schools, timing of movements at the PIT tag antenna array, and differences in time spent in the river by females and males indicated that visual spawning surveys during daylight hours may not fully represent the entire spawning population.

The spatial distribution of spawning pygmy whitefish is limited to a narrow reach of habitat within the tributaries of CML, despite fish having access to additional upstream habitat. Pygmy whitefish schools were concentrated within the first 3.0 km of the Cedar River, and the first 2.0 km on the Rex River. In addition, floodplain or sidechannel habitat was not used in either river system demonstrating that in this system, pygmy whitefish occurred only in main-stem habitat with low gradients (< 1%) where substrate was comprised primarily of gravel. At the upper end of the spawning distribution for pygmy whitefish, gradient and substrate size increased possibly creating less favorable spawning conditions. Even within the primary spawning reach, schools of fish were concentrated to a short 800 m reach in a given year further suggesting that the range of habitat where eggs were dispersed was narrow, and at least in this system, influenced by proximity to the lake. It represents vital habitat that should be protected for this species when developing management plans in the Cedar River Municipal Watershed. While the majority of pygmy whitefish were detected in the Cedar River, the presence of schools in the Rex River demonstrated that at least a portion of reproduction each year was dispersed between tributaries of CML, thereby increasing the overall spawning area.

The strategy of spawning in habitat immediately upstream of the lake could be related to many factors including favorable egg incubation sites, lower gradient habitat with decreased risk of scour (Shellberg 2002), or simply a reduction in the distance fish migrate upstream to spawn. Or, perhaps, pygmy whitefish are generally vulnerable to predation in shallow stream habitat and therefore moved upstream mainly under the cover of darkness. Although we did not definitively determine egg deposition sites, it is logical that fish spawned within the reaches where schools were observed during spawning surveys. Preliminary field evidence suggests that pygmy whitefish release eggs in flowing water where they drift downstream before settling into incubation habitat, or that eggs continue drifting to pelagic habitat, similar to broadcast spawning stream cyprinids in the west-central United States (Altenbach et al. 2000). By using habitat in close proximity to the lake, eggs settle in low-gradient stream habitat or near the lake/river confluence, and upon hatching in early spring (Barnett and Paige 2012) young fry are better positioned to outmigrate to productive pelagic habitat to begin feeding and growing. Additionally, as our capture of spawning schools indicated, most of the fish present in daytime spawning schools were male. If females move into the river habitat in a single night to deposit eggs, they would likely select habitat near the lake and consequently males would hold in this habitat to increase the likelihood of finding a mate.

Pygmy whitefish schools were observed in the river for several weeks each year at the beginning of December, indicating that the duration of the spawning period is also relatively narrow. By moving into the river after the greatest threats of fall rains decline, pygmy whitefish minimize the risk of being in river habitat during high flows. Although the average river temperature did not change dramatically (2.7–5.1 ºC), streamflow and temperature are important factors determining the variation in timing of the annual spawning migration for many salmonids (Gillet 1991, Knapp and Vrendenburg 1996). Average streamflow varied annually for the Cedar River, but it was generally stable late in the year while pygmy whitefish spawned, because most precipitation falls as snow by early December, possibly contributing to pygmy whitefish spawning success. Temperature also declines to seasonal lows at this time of year, and as Price (1940) suggested, whitefish may be adapted to incubate most successfully at these low stream temperatures. Although stream conditions may be more predictable at this time of year, the compact spawning period makes the entire cohort vulnerable to the same set of environmental risks (e.g., late season floods), and spawning in multiple tributaries of a lake system (e.g., Cedar and Rex rivers) may increase the variation in habitat conditions for incubation.

In addition to characterizing the spatial and temporal distribution of spawning, the presence of spawning schools in the river provided an opportunity to investigate characteristics of spawning schools and to mark individual fish. Capture of pygmy whitefish from a single spawning school during daylight hours (0800 to 1600) revealed that the overwhelming majority of fish in these groups were male. Collection efforts were designed to capture an entire school, and to sample throughout the run to avoid differences in run timing between sexes, and although a few individuals escaped seine nets, the sex ratio of schools was highly disproportionate in all cases. Not only was the proportion of females significantly less in all the schools sampled, females spent significantly less time in the river during the spawning run than males as determined by individual PIT tag detections. It is possible that the extremely high proportion of males made finding a mate easy for females resulting in a short instream spawning period. Males in other salmonid populations (both broadcast spawning and species that construct redds) often arrive on spawning grounds earlier and spend more time than females (Beauchamp 1990, Hutchings and Gerber 2002, Anderson and Quinn 2007). However, the discrepancy in sex-ratio during daytime hours and residence time discovered for pygmy whitefish between sexes appears different than other stream broadcast spawning species such as the peppered chub (*Macrhybopsis tetranema*) (Wilde and Durham 2008). Sex-ratio of adult pygmy whitefish captured from Dina Lake #1 showed twice as many females as males (Zemlak and McPhail 2004). A clear understanding of how differences in migration behavior for females and males could affect visual counts is necessary to consider before applying methods such as area-under-the-curve (AUC) estimates as a potential monitoring strategy for the spawning population (Parsons and Skalski 2010).

Since visual spawning surveys and fish collection efforts were conducted during daylight hours, it is possible that pygmy whitefish sex ratios are different at nighttime. Heard and Hartman (1966) reported pygmy whitefish moving into riverine habitat to spawn only at nighttime in the Brooks River, Alaska. Increased activity levels during evening hours are also commonly reported for other salmonid species (Piecuch et al. 2007, Barnett and Paige 2013) and in fact, detections at the PIT tag array confirmed increased movement during nighttime hours. Visual spawning surveys conducted during daylight hours may only sample a portion of the spawning pygmy whitefish population. Evening capture sessions of pygmy whitefish spawning schools to determine if females move into the river during a single evening excursion, or are more abundant during nighttime hours, could help explain the sex ratio differences observed on the spawning grounds in this study.

Marking of individual pygmy whitefish with PIT tags allowed characterization of specific movement patterns for individuals and provided results to evaluate differences in observed daytime sex ratios of schools. However, it should be noted that female pygmy whitefish could shed PIT tags at a higher rate than males during spawning. A study of coastal cutthroat trout (*Oncorhynchus clarki clarki*) indicated that fish tagged at a larger size expelled PIT tags at a higher rate than fish tagged at smaller sizes, and that a number of the shed PIT tags were recovered at redd sites suggesting they were expelled during spawning activity (Bateman et al. 2009). Prentice et al. (1990) also found that spawning female Atlantic salmon (*Salmo salar*) expelled PIT tags at a higher rate than males or non-spawning females. Together, these studies show that PIT tag expulsion can occur during spawning and it is possible that pygmy whitefish, particularly females, expelled PIT tags while spawning in this study. In this case, our study would underestimate female return rates through PIT tag detections. Alternatively, the energetic investment required for gamete production by females may lead to a higher mortality rate (Hayward and Gillooly 2012), which could also explain the discrepancy we found in survival between sexes. Other sources of mortality on tagged fish include loss associated with the tagging process and predation by adult bull trout in CML (Connor et al. 2001).

Although the sample of returning females through PIT tag detections was relatively low, individual records for returning fish provided valuable insight into movement patterns including residence time during the spawning season. The median amount of time spent in the river for female pygmy whitefish was approximately one day suggesting that females may move into river habitat and deposit eggs quickly. Detections at the PIT tag antenna array indicated that the majority of upstream movement for both female and males occurred during nighttime hours. Perhaps females move into the river during nighttime hours, when the risk of predation from common predators (e.g., osprey, eagles, otters) in riverine habitat may be somewhat reduced, complete the act of spawning at night, and then return to the more protective cover of the deep lake. The low proportion of females in spawning schools coupled with a reduced residence time for individual female pygmy whitefish supports this theory.

Recapture of individually tagged pygmy whitefish from spawning schools at least one year post-tagging showed that the growth of reproductive aged fish was extremely limited in this population, similar to other systems (Eschmeyer and Bailey 1955, Zemlak and McPhail 2004). Data from McLure Lake in British Columbia, Canada found that 50% of males and 75% of females matured by age three, and in Brooks and South Bay Lakes, Alaska more than 95% of all fish were mature by age two (Wydowski and Whitney 2003). In Dina Lake #1, a closed lake system, near Mackenzie, British Columbia, males matured at age three and females at age four (Zemlak and McPhail 2004). Most spawning pygmy whitefish in the CML population are at least age three or age four (SPU unpublished data) suggesting similar development timing as McLure and Dina Lake #1 pygmy whitefish. Return of individuals at the PIT tag antenna array documented that an individual may spawn in at least six consecutive years. Using an estimate of initiating spawning at age three, older individuals are expected to be age eight or age nine and nearing the upper limits of life expectancy for the species (McPhail and Zemlak 2001, Wydowski and Whitney 2003). The use of scales to age fish is not a preferred method (Casselman 1987) and tends to underestimate age (Zemlak and McPhail 2004), and therefore, age nine represents a minimum age limit for fish in CML. Recapture of pygmy whitefish indicates that very little growth occurs in years after reproductive condition is reached, suggesting that most energy is invested in gamete production.

Detections of pygmy whitefish at the PIT tag antenna array one year post-tagging represent a minimum survival estimate for the tagged population for several reasons. One explanation for the observed variation in return rates could be related to how the PIT tag antenna array functioned. For instance, a few pygmy whitefish spawn downstream of the PIT tag antenna array on the Cedar River (e.g., 2011); therefore, some tagged fish would not be detected moving past the antenna array in subsequent years. The possibility of lake spawning, similar to a population in northern British Columbia (Eschmeyer and Bailey 1955, Zemlak and McPhail 2004) also exists for this population but has not been documented. Expulsion of PIT tags has been documented in other spawning populations (Prentice et al. 1990, Bateman et al. 2009, Dieterman and Hoxmeier 2009, Meyer et al. 2011), and could lead to underestimation of returning individuals. In addition, fish moved between tributary systems of the lake (Rex River to Cedar River) showing that some individuals stray from their stream of initial tagging. A PIT tag antenna array was present on only one tributary of CML, so non-detection could occur if a fish moved between tributary river systems. Non-detections might also occur due to antenna related issues such as mechanical failures and inefficiencies or high flows at time of movement. However, flows remained relatively low during all six years when tagged fish returned and antennas functioned under these conditions. In addition, fish were observed moving upstream by hovering over the streambed, even in higher flows, and therefore it is expected that fish moving upstream at the PIT tag array were detected because the antenna was secured to the streambed. Finally, if more than one tagged individual crossed a single antenna at the same time, neither would be detected. Because pygmy whitefish congregate in schools, this behavior should be considered as another possible reason for not detecting an individual.

Investigating broadcast spawning pygmy whitefish in tributaries of CML provided valuable insight into the basic reproductive ecology of this species. Our results demonstrate that at least for this population, riverine spawning habitat is concentrated within a narrow distribution in close proximity to pelagic habitat. Many factors could adversely affect spawning habitat used by pygmy whitefish including land management practices, localized scour from a high flow event, shifts in stream channel configuration stranding eggs, and potentially climate change (Mote et al. 2008; Lawler et al. 2010). In reservoir systems, like CML, the timing and extent of inundation and drawdown could also affect survival of pygmy whitefish eggs during the incubation period. The level of CML typically rises through the pygmy whitefish incubation period providing protection to eggs from desiccation; however, in other reservoir systems, elevations during incubation should be evaluated for potential effects. The narrow spatial and temporal distribution of spawning for pygmy whitefish is important to consider in management or conservation of habitat throughout the species range and contributes valuable insight into this broadcast spawning species. Much basic life history information is largely unknown for pygmy whitefish and the available literature associated with spawning is limited to the timing of reproduction and general location of spawning (e.g., Heard and Hartman 1966, Hallock and Mongillo 1998, Zemlak and McPhail 2004). By tagging individual fish, we documented that pygmy whitefish return to spawn in multiple years and that diel sex-specific behavior occurs during the spawning run. Collectively, these results could assist in developing a predicative life-history model for pygmy whitefish or similar riverine broadcast spawning species.

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