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ECOLOGY OF UNIQUE LENTIC POPULATIONS OF ROUNDTAIL CHUB, *GILA ROBUSTA*

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Abstract.—Although roundtail chub (*Gila robusta*) is generally considered a riverine species, 6 natural lakes in the upper Green River basin, Wyoming, have resident populations of this fish. In 2 of the lakes, Halfmoon and Little Halfmoon, we investigated the ecology of resident roundtail chub, including their habitat use, diet, weight–length relationships, growth, and reproduction. Lentic roundtail chub used littoral and mid-depth benthic habitats most often, with the highest catch rates in littoral habitats. Roundtail chub were rarely caught in pelagic or deep benthic habitats. Opportunistic foraging was observed in both lakes, with roundtail chub consuming terrestrial and aquatic insects, vegetation, and fish. Roundtail chub from both lakes had weight–length relationships similar to those reported for lotic populations but slower annual growth rates. Fish in spawning condition were captured from mid-June to late July when water temperatures ranged from 8.7 to 18.3 °C and snowmelt runoff was at its maximum. Knowledge of roundtail chub ecology in lentic systems will influence management decisions and conservation actions important to preserving this species in the Colorado River basin.

Resumen.—A pesar de que la carpita cola redonda (*Gila robusta*) se considera generalmente una especie de río, seis lagos naturales en la cuenca alta del Río Green, Wyoming tienen poblaciones residentes de este pez. En dos de los lagos, Halfmoon (Media luna) y Little Halfmoon (Pequeña media luna), investigamos la ecología de carpitas cola redonda residentes, incluyendo su uso de hábitat, dieta, la relación entre peso y longitud, crecimiento y reproducción. Las carpitas cola redonda lénticas usaron hábitats litorales y bentónicos de mediana profundidad más a menudo, con las mayores tasas de captura en los hábitats litorales. Las carpitas cola redonda se capturaron raramente en en hábitats pelágicos o bentónicos profundos. En ambos lagos se observó un forrajeo oportunista, en donde la carpita consume insectos terrestres y acuáticos, vegetación y peces. Las carpitas provenientes de ambos lagos tuvieron una relación peso-longitud similar a la reportada en poblaciones lóticas, pero con tasas de crecimiento anual más lentas. Se capturaron peces en condiciones de desove desde mediados de junio hasta finales de julio, cuando la temperatura en el agua osciló entre 8.7 y 18.3 °C, y cuando el derretimiento de la nieve estaba en su máximo. El conocimiento de la ecología de la carpita cola redonda en sistemas lénticos ayudará a influí en las decisiones de manejo y en las acciones para la conservación, las cuales son importantes para preservar esta especie en la cuenca del Río Colorado.

Roundtail chub (*Gila robusta*) is endemic to the Colorado River basin and is widely recognized as a riverine fish (Minckley and Deacon 1968, Bezzerides and Bestgen 2002). However, the species is not restricted to lotic systems. A few endemic populations inhabit natural lakes where they may have unique evolutionary and conservation value (Moritz 1994, Kern et al. 2007).

Once abundant in the Colorado River basin, roundtail chub remain in only 45% of their historical range (Bezzerides and Bestgen 2002). This rangewide decline is due to dams, water diversions, and nonnative fish introductions (Minckley and Deacon 1968, Bezzerides and Bestgen 2002, Olden and Poff 2005, Gill et al. 2007). Roundtail chub is listed as a species of concern in Arizona, Colorado, and Wyoming, as threatened in Utah and endangered in New Mexico (Bezzerides and Bestgen 2002), and as a candidate for listing in the lower Colorado River basin under the Endangered Species Act (USFWS 2009).

Lotic populations are harmed by reservoirs and water diversions that fragment populations, alter habitat, and serve as refuges for exotic species (Bestgen and Propst 1989, Martinez et al. 1994, Compton et al. 2008). Roundtail chub declines in impoundments are common after reservoir construction (Martinez et al. 1994, Bezzerides and Bestgen 2002), but the species appears to persist in some Colorado reservoirs (J. Logan, Colorado Division of Wildlife, personal communication; Ewert 2010). However, this persistence may be due to immigration from nearby stream populations.

Lentic populations of roundtail chub exist in 6 natural lakes of the upper Green River basin

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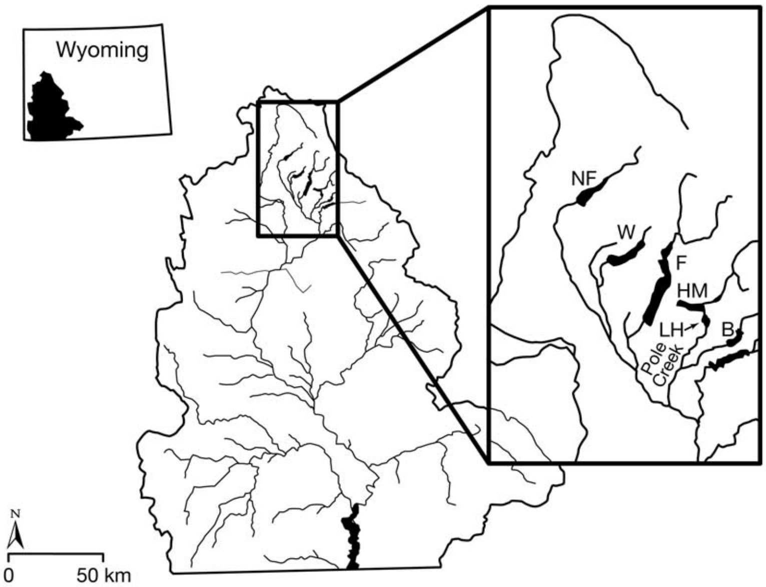

Fig. 1. Lakes of the upper Green River basin, Wyoming, with populations of roundtail chub: New Fork Lake (NF), Willow Lake (W), Fremont Lake (F), Halfmoon Lake (HM), Little Halfmoon Lake (LH), and Burnt Lake (B). Halfmoon and Little Halfmoon lakes were sampled for roundtail chub during this study.

(Kern et al. 2007). Although small dams have been constructed on 4 of the 6 lakes (Tyrrell 2011), these are the only naturally formed lakes in the Colorado River basin where roundtail chub populations occur. Roundtail chub in these lakes are isolated from all other populations of roundtail chub because they are upstream of Fontenelle Dam in Wyoming. These lentic populations are the only ones upstream of Fontenelle Reservoir, as well as the only known natural lake-dwelling populations of this species. These populations are not exposed to the same physiochemical perturbations as lotic populations because dams and water diversions have not altered their environment. Nonetheless, naturalized populations of nonnative predatory fishes such as lake trout (*Salvelinus namaycush*) and brown trout (*Salmo trutta*) may pose a risk to roundtail chub in these natural lakes.

Because roundtail chub have been extirpated from at least one lake (Boulder Lake, Sublette County, WY; Miller 1977, Rhea 2008), there is a need for information on remaining populations. This information could guide management actions, such as the establishment of new populations by translocation. The purpose of this article is to describe basic ecological information on endemic roundtail chub populations in natural lakes, including habitat use, weight–length relationships, growth, and reproduction. We also compare data from these lentic populations with previously published information for lotic populations.

Study Area

Roundtail chub in 2 of the 6 natural lakes with endemic populations were selected for study (Fig. 1). Halfmoon and Little Halfmoon lakes, Sublette County, Wyoming, are in the Pole Creek drainage and connected by 400 m of stream. Halfmoon Lake is upstream of Little Halfmoon Lake. In addition to roundtail chub, both lakes have lake trout, brown trout, rainbow trout (*Oncorhynchus mykiss*), mountain whitefish (*Prosopium williamsoni*), white sucker (*Catostomus commersonii*), flannelmouth sucker (*Catostomus latipinnis*), hybrids of white sucker and flannelmouth sucker, mountain sucker (*Catostomus platyrhynchus*), mottled sculpin (*Cottus bairdii*), speckled dace (*Rhinichthys osculus*), and redside shiner (*Richardsonius balteatus*). Halfmoon Lake also has lake chub (*Couesius plumbeus*).

Halfmoon Lake has a surface area of 4.3 km^2, maximum depth of 85 m, and surface elevation of 2316 m. The southeast arm of the lake has depths <30 m, with a gently sloping shoreline compared to the steeper northern and southern shorelines (Leopold 2000). The substrate over much of the lake bottom is unknown, but numerous rocky outcrops occur along the southern and northern shoreline. There are several sandy beaches around the lake: one in the southern arm near Pole Creek's exit from the lake, another near Pole Creek's entrance to the lake, and one along the western shore.

Little Halfmoon Lake has a surface area of 0.24 km^2, maximum depth of 17 m, and surface elevation of 2315 m. The northern half of the lake is shallow (<2.5 m), with deep water (>15 m) in a narrow area on the south end of the lake. During late spring and early summer, inflowing currents from Pole Creek are evident along the eastern shore of the lake. The substrate is dominated by silt and sand, with isolated patches of dense vegetation in water <4 m deep. The southern shore of the lake has large rock and boulder substrate with water depths <1 m.

METHODS

Halfmoon and Little Halfmoon lakes were sampled on alternate weeks from June to August 2008 and from May to August 2009. Sampled habitats included littoral with cover, littoral with no cover, mid-depth benthic, deep benthic, surface pelagic, and deep pelagic. Littoral habitats with cover and littoral habitats with no cover were located in the littoral zones of each lake in depths <6 m. Littoral habitat with cover was defined by boulders, wood, or macrophytes, while littoral habitat without cover had bare sand or gravel substrate. Mid-depth benthic habitat was between 9 and 12 m deep, with unknown substrate. Deep benthic habitat was sampled over unknown substrate at a depth of 30 m in Halfmoon Lake and 15 m in Little Halfmoon Lake. In the pelagic zone, surface pelagic habitat was sampled from the surface to 6 m deep, and deep pelagic habitat from 6 m to 12 m deep.

Overnight gill-net sets of 3 mesh sizes (19, 25, and 32 mm bar mesh) were set to capture roundtail chub. Gill nets were made up of a single-mesh panel (15.2 × 1.8 m) in various combinations for sampling different habitats within the lakes. Single-mesh panel gill nets were used to sample littoral habitat with cover, littoral habitat without cover, and mid-depth benthic habitat in both years. Surface pelagic and deep pelagic habitats were sampled with a multimesh panel (total dimensions 45.7 m × 5.5 m), each mesh size comprising one-third of the total net area. Deep benthic habitat was sampled with a multimesh panel (total dimensions 45.7 m × 1.8 m), with all sizes tied together. Surface pelagic habitat was sampled only in 2008 and deep benthic habitat only in 2009. Deep pelagic habitat was sampled in both years.

In Halfmoon Lake, 6 sites of each habitat were sampled, 3 sites in each year, except surface pelagic and deep benthic habitats, which were sampled only one year at 3 sites. In Little Halfmoon Lake, the same 3 sites for littoral habitats with and without cover and mid-depth benthic habitat were sampled in both years due to the small size of the lake. Also, 2 sites for the pelagic habitats were sampled in 2008 and one site each for deep benthic and deep pelagic habitats in 2009. Gill nets were set overnight every other day, and mesh sizes were rotated among the sites so that one mesh size did not sample a site more than once in a week.

Each site was sampled 2 times before and 2 times after thermal stratification. To determine when and at what depth stratification occurred, temperature profiles were obtained by lowering a temperature probe (Model YSI-550A, Yellow Springs Instruments, Yellow Springs, OH) from the surface in 1-m increments to a 12-m depth in both lakes in 2008, and to a 30-m depth in Halfmoon Lake and to the bottom (15 m) in Little Halfmoon Lake in 2009.

Analysis of natural log–transformed catch-per-unit-effort (CPUE = fish · 100 $m^{-2}h^{-1}$) data was performed in JMP 8 (SAS Institute, Inc., Cary, NC). To test for differences between sampling years and sampling periods, the general linear model (GLM) was used with sampling year, habitat type, and sampling period as independent variables, and an independent analysis was conducted for each lake. One-way ANOVA was used to test for differences in CPUE among habitats. The post hoc Tukey–Kramer honestly significant difference (HSD) test was used to determine if there were significant differences between the 3 habitat types included in the model: littoral with cover, littoral with no cover, and mid-depth benthic. An alpha value of 0.05 was used for all tests.

We weighed (in grams) and measured (total length [TL] in millimeters) all roundtail chub. Live roundtail chub were released. Fish that perished in the nets were frozen, and stomachs were removed later to determine gut contents.

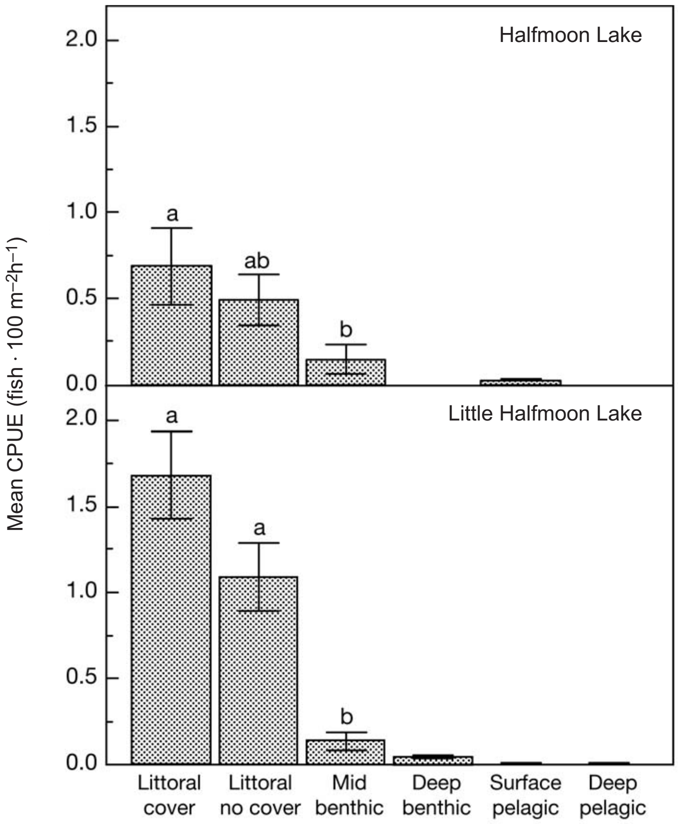

Fig. 2. Mean catch-per-unit-effort (CPUE) of roundtail chub in Halfmoon Lake and Little Halfmoon Lake. Error bars represent one standard error. Tukey–Kramer HSD designations are shown above the bars for 3 habitats: littoral with cover, littoral with no cover, and mid-depth benthic.

All items in stomachs were enumerated and preserved in 95% ethanol. To increase sample size for diet analysis, additional roundtail chub were captured from littoral and mid-depth benthic habitats of Halfmoon Lake in August 2010. All fish were handled in the same way as fish caught in 2008 and 2009. Stomach contents of roundtail chub were summarized by percent occurrence of fish with particular taxa in their stomachs. Frequency distributions for lengths of roundtail chub were examined, and log weight–length relationships (Log W = a + b * Log TL) were computed for each lake by fitting a regression line based on all fish captured during the study (JMP 8). Growth estimates (mm · year^{-1}) for roundtail chub were calculated from recaptures of Floy-tagged fish marked in Little Halfmoon Lake by the Wyoming Game and Fish Department in previous years. We noted any roundtail chub that were in spawning condition (males that expressed milt or females that expressed eggs when gently squeezed) and recorded the date, capture location, and water temperature for these fish.

RESULTS

Habitat

Temperature profiles indicated that thermal stratification began in early to mid-July in Halfmoon and Little Halfmoon lakes. We considered fish captured before stratification as sampled in the thermally-mixed period and those captured after stratification as sampled in the thermally-stratified period. Roundtail chub were primarily captured in littoral habitats, both those with and without cover, as well as in mid-depth benthic habitats; so these were the only habitats included in the analysis. Roundtail chub were rarely captured in deep benthic, surface pelagic, and deep pelagic habitats (Fig. 2). Year (GLM: Halfmoon Lake, $P = 0.702$; Little Halfmoon

Lake, $P = 0.301$) and sampling period (Halfmoon Lake, $P = 0.592$; Little Halfmoon Lake, $P = 0.427$) were not significant variables accounting for variation in CPUE, indicating that roundtail chub did not change their habitat use between years or as lakes became stratified during summer. Consequently, data from both years and both sampling periods were combined for further analysis of habitat use.

In both lakes, roundtail chub CPUE was highest in littoral habitats, indicating greater use of these areas (one-way ANOVA: Halfmoon Lake, $P = 0.023$; Little Halfmoon Lake, $P < 0.001$). Although there was a trend for CPUE to be higher in littoral habitats with cover than in littoral habitats without cover (Fig. 2), these differences were not statistically significant (Tukey–Kramer HSD: Halfmoon Lake, $P = 0.753$; Little Halfmoon Lake, $P = 0.084$). In Halfmoon Lake, CPUE in littoral habitat with cover was significantly greater than CPUE in mid-depth benthic habitat (Tukey–Kramer HSD: $P = 0.021$), but CPUE in littoral habitat without cover was not significantly different from mid-depth benthic habitat (Tukey–Kramer HSD: $P = 0.116$). These results indicate a gradient of relative abundance of roundtail chub from littoral habitats with cover to littoral habitats without cover to mid-depth benthic habitats. In Little Halfmoon Lake, CPUE in both littoral habitat with cover and littoral habitat without cover was significantly greater than in mid-depth benthic habitat (Tukey–Kramer HSD: with cover, $P < 0.001$; without cover, $P < 0.001$), indicating higher use of littoral habitats by roundtail chub in this lake.

Diet

Contents of 43 stomachs from fish in Halfmoon Lake and 57 stomachs from fish in Little Halfmoon Lake were analyzed. Ten roundtail chub from Halfmoon Lake and 18 roundtail chub from Little Halfmoon Lake had empty stomachs. Terrestrial insects were the predominant prey type in stomachs (Fig. 3). Roundtail chub also consumed Trichoptera, vegetation, Diptera, Ephemeroptera, and fish. The proportions of roundtail chub with specific taxa in their stomachs varied between the 2 lakes, which may indicate differences in food availability between lakes and opportunistic feeding by roundtail chub. Piscivory was rare; only 2 roundtail chub of 252 and 315 mm TL consumed one fish each.

Weight–Length Relationships and Growth

The mean total length of roundtail chub captured in Halfmoon Lake was 211 ± 5 mm (n = 223, range 120–340 mm TL). The log-weight versus log-length relationship for roundtail chub in Halfmoon Lake was

$$\text{Log W} = -5.273 + 3.078 * \text{Log TL},$$

where weight (W) was measured in grams and TL was measured in millimeters ($SE_a = 0.131$, $SE_b = 0.056$, $n = 166$, $r^2 = 0.95$, $P < 0.0001$). In Little Halfmoon Lake, the mean total length of captured roundtail chub was 212 ± 4 mm (n = 333, range 158–375 mm TL). The log weight versus log length relationship for roundtail chub in Little Halfmoon Lake was

$$\text{Log W} = -5.032 + 2.973 * \text{Log TL},$$

where weight (W) was measured in grams and TL was measured in millimeters ($SE_a = 0.091$, $SE_b = 0.039$, $n = 317$, $r^2 = 0.95$, $P < 0.0001$). No significant difference was found between the regression lines for fish from the 2 lakes ($P = 0.697$). Mean annual growth of adult roundtail chub was calculated as 20.4 ± 3.5 mm TL, based on recapture data from 21 fish in Little Halfmoon Lake. Tagged fish ranged from 121 to 216 mm TL at initial capture.

Reproduction

Forty-two roundtail chub in spawning condition were captured in Halfmoon and Little Halfmoon lakes between 19 June and 29 July when water temperatures ranged from 8.7 to 18.3 °C. The largest catch of fish in spawning condition ($n = 16$) occurred approximately midway between the inlet and outlet of Little Halfmoon Lake on 26 June 2009, in littoral habitat with sand substrate when the water temperature was 10.5 °C and the lake was not stratified. Current from the inflow of Pole Creek was evident at this location. Capture of fish in spawning condition corresponded with the peak and descending limb of snowmelt runoff (USGS gauge data, 09205000 New Fork River, near Big Piney, Wyoming). The mean length of females in spawning condition was 241 ± 37 mm TL ($n = 9$) with a mean weight of 120 ± 78 g ($n = 7$). Males in spawning condition were smaller, with a mean length of 200 ± 8 mm TL ($n = 33$) and mean weight of 66 ± 8 g ($n = 32$). The smallest spawning female captured had a

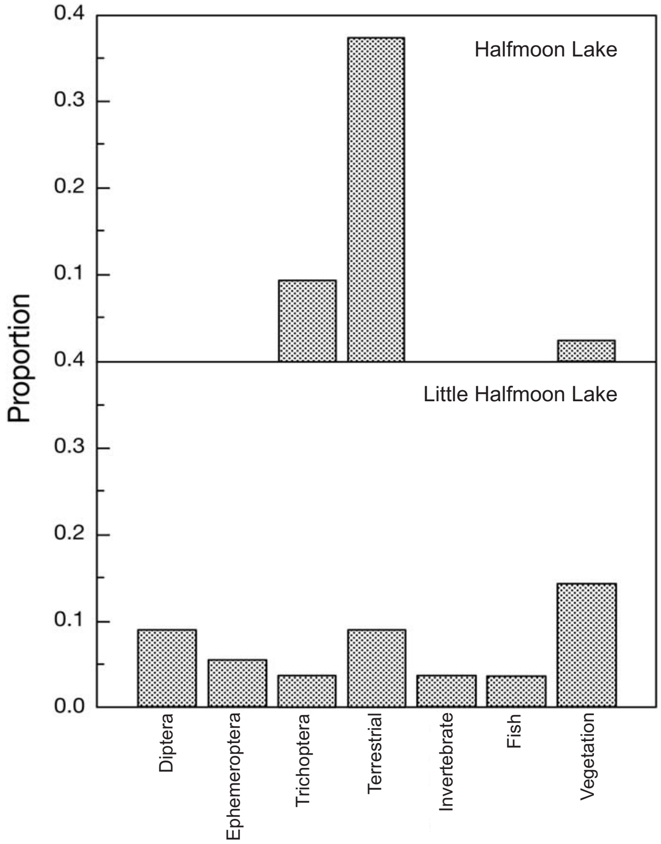

Fig. 3. The proportion of sampled roundtail chub in Halfmoon Lake and Little Halfmoon Lake that consumed a given item. The category labeled "invertebrate" refers to unidentified insects of either terrestrial or aquatic origin.

length of 180 mm TL, and the smallest spawning male had a length of 168 mm TL.

Discussion

Roundtail chub in Halfmoon and Little Halfmoon lakes predominantly used littoral habitats with or without cover. Littoral habitats in the lakes have low to zero current velocity and a variety of substrate and cover types that may create conditions similar to those of pool habitat in streams, where roundtail chub are known to occur (Bestgen 1985, Barrett and Maughan 1995, Bottcher 2009). In some streams, loss of pool habitat or low densities of pools are a limiting factor for roundtail chub (Bower et al. 2008, Bottcher 2009). In addition to pools, roundtail chub use a variety of habitat features, including boulder, gravel, and sand substrates; overhanging and submerged vegetation; and wood debris (Bestgen and Propst 1989, Barrett and Maughan 1995, Brouder et al. 2000)—all of which are present in the littoral zones of Halfmoon and Little Halfmoon lakes. The array of habitat features is important to roundtail chub, and in stream systems the roundtail chub's abundance is related to habitat diversity (McAda et al. 1980, Bestgen and Propst 1989, Bottcher 2009). Because habitat diversity is critical for roundtail chub population persistence in stream systems (McAda et al. 1980, Bestgen and Propst 1989, Bottcher 2009), it is likely critical in lake systems as well.

Roundtail chub adults in lotic systems have been described as omnivorous (Vanicek and Kramer 1969, Greger and Deacon 1988, Quist et al. 2006), and we found that roundtail chub diets in the 2 natural lakes were similar to those described for lotic systems. Roundtail chub in Muddy Creek, Wyoming (Quist et al. 2006), and the Green River, Utah (Vanicek and Kramer 1969), consumed terrestrial insects, vegetation, aquatic insects, and fish. Roundtail chub in lotic systems have been observed to become piscivorous at 100 mm TL (Vanicek and Kramer 1969, Quist et al. 2006), but piscivory by roundtail chub <250 mm TL was not observed in fish sampled from the 2 natural lakes during this study. The Wyoming Game and Fish Department observed piscivory in roundtail chub as small as 213 mm TL in Little Halfmoon Lake, but fish smaller than this were not examined (Wyoming Game and Fish Department, unpublished data). Percent occurrence of fish in the diets of roundtail chub in lotic systems has ranged from 8% to 15% (Vanicek and Kramer 1969, Quist et al. 2006), while percent occurrence of fish in roundtail chub stomachs we sampled was merely 2%. However, the Wyoming Game and Fish Department has observed piscivory in 23% of sampled roundtail chub from Little Halfmoon Lake (Wyoming Game and Fish Department, unpublished data). Discrepancies in proportions of piscivorous roundtail chub and total length when piscivory begins were observed for roundtail chub in the study lakes. Further investigation is needed to elucidate this relationship, as our sample sizes were relatively small.

Comparison of weight–length regressions showed no evidence that body condition of roundtail chub in the 2 lentic populations differed from body condition of roundtail chub in lotic populations. The weight–length regression lines from fish sampled from the Halfmoon Lake roundtail chub population were not significantly different from those in the Green River, Utah (within 95% confidence limits; Vanicek and Kramer 1969), and the Verde River, Arizona (Brouder et al. 2000), populations. The same was observed for roundtail chub from Little Halfmoon Lake and the Verde River. In some cases, a fish species adapted to lotic environments, such as roundtail chub, may exhibit reduced body condition in lentic systems (Kruse and Hubert 1997, Rypel et al. 2006), but this pattern was not evident for roundtail chub in the 2 natural lakes.

Information regarding roundtail chub growth is sparse, with no information on growth in the upper Colorado River basin or in lentic environments. The growth rates observed in Little Halfmoon Lake were less than those observed in the Verde River, Arizona, where fish of similar lengths grew an additional 13 mm per year (Brouder et al. 2000). Because growth rates in fish are dependent on temperature, this discrepancy may be due to the colder summer water temperatures and shorter growing season in the study lakes compared to temperatures and season length at lower-elevation and lower-latitude sites in Arizona.

The time of year when roundtail chub are reproductively active may depend on their location in the Colorado River basin, as dictated by water temperatures and timing of runoff. Roundtail chub in the lower Colorado River basin have been found in spawning condition from mid-April to mid-May (Brouder et al. 2006), while fish in the upper basin appear to spawn from mid-May to late July (Vanicek and Kramer 1969, Kaeding et al. 1990, Karp and Tyus 1990). The threshold water temperature for roundtail chub to reproduce has been estimated at 18 °C (Vanicek and Kramer 1969). However, roundtail chub in spawning condition have been captured at 14.5 °C in the Yampa and Green rivers, Colorado (Karp and Tyus 1990), and were observed beginning at 8.7 °C in Little Halfmoon Lake, which greatly reduces the previous estimate of water temperature threshold for spawning. Reports from the upper Colorado River basin consistently describe roundtail chub to be in spawning condition during the peak and descending limb of the hydrograph associated with the period of spring runoff (Kaeding et al. 1990, Karp and Tyus 1990). Because roundtail chub reproduce at a wide range of temperatures throughout the basin, peak runoff may be a critical cue for roundtail chub to reproduce.

Knowledge of roundtail chub ecology in these natural lentic systems can aid in developing management and conservation actions for resident populations in lakes and reservoirs. Further study is needed to elucidate the relationship between age and length for roundtail chub in the lakes and to understand how these populations compare with others in the basin in regards to diet composition and timing of reproduction. It would also be beneficial to explore mechanisms responsible for the extirpation of roundtail chub from Boulder Lake, particularly the interaction between nonnative predators and habitat conditions. With the information we have gathered, translocation and establishment of roundtail chub populations in new lentic habitats should be possible, since this species is able to survive, grow, and reproduce in the lakes we studied. Our data indicate that roundtail chub can reproduce at colder temperatures than were recorded for most populations previously studied (Vanicek and Kramer 1969, Karp and Tyus 1990, Brouder et al. 2000) and that roundtail chub can live at high elevations (Bezzerides and Bestgen 2002). If roundtail chub are relocated to additional lakes or if new reservoirs are constructed, suitable habitat such as extensive littoral areas with habitat diversity should be available to meet their life history needs.

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