Transactions of the American Fisheries Society 143:519–527, 2014
© American Fisheries Society 2014
ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2013.869258

ARTICLE

Movement and Growth of Juvenile Colorado Pikeminnows in the San Juan River, Colorado, New Mexico, and Utah

Scott L. Durst*
U.S. Fish and Wildlife Service, San Juan River Basin Recovery Implementation Program, New Mexico Ecological Services Field Office, Albuquerque, New Mexico 87113, USA

Nathan R. Franssen
Department of Biology and Museum of Southwestern Biology, University of New Mexico, 167 Castetter Hall, Albuquerque, New Mexico 87131, USA

Downloaded by [US Fish & Wildlife Service] at 05:58 17 November 2015

Abstract
Understanding patterns of animal distribution and abundance based on their movements is important to identify the habitats and factors that maximize growth and reproductive success. Despite stocking age-0 hatchery-reared Colorado Pikeminnow *Ptychocheilus lucius* for over 10 years in the San Juan River of Colorado, New Mexico, and Utah, the population consists primarily of stocked juveniles; adults remain rare. We investigated seasonal movement and growth of juvenile Colorado Pikeminnows in the San Juan River from 2009 to 2012 to inform recovery efforts throughout the Colorado River basin. Our results indicated fish made long-distance upstream movements from spring to summer while moving back downstream over winter. Seasonal movements may be associated with maximizing growth along longitudinal and seasonal temperature regimes. Length-at-age relationships reveal Colorado Pikeminnows in the San Juan River were larger than individuals of the same age in other populations in the upper Colorado River basin. While warmer water temperatures may have played some role in the larger lengths at age we observed, the hatchery-reared fish that are stocked at age 0 are probably larger than their wild-spawned counterparts of the same age. Variation in growth rates among size-classes indicates small Colorado Pikeminnows (<200 mm TL) had slower growth rates than larger individuals in the San Juan River, suggesting a possible resource limitation for smaller juvenile fish. Understanding how seasonal movement and growth of all life stages of Colorado Pikeminnow interact with modified river systems will be important for population conservation and recovery efforts in the upper Colorado River basin.

Patterns of animal distribution and abundance can be based on their movement and selection of habitats (Tyler and Rose 1994; Gowan and Fausch 2002), and successful growth and reproduction often require age-specific resources that can vary among habitats. Ideally, animals should move to habitats that offer the best prospects for growth, survival, and reproduction (Fausch 1984; Montgomery et al. 1991; Hughes 1998; Krivan 2003), while simultaneously avoiding predation and competition (Harvey 1991; Hughes 1992; Moody et al. 1996; Magoulick 2004; Ward et al. 2006). Understanding how habitat alteration and fragmentation may affect movement and other life history characteristics of endangered species should help managers develop strategies for their conservation and recovery.

The federally protected Colorado Pikeminnow *Ptychocheilus lucius* is a large piscivorous cyprinid endemic to the Colorado River basin in the southwestern USA (USFWS 1967; Tyus 1991). Wild and self-sustaining populations are limited to areas upstream of Lake Powell, Arizona and Utah, in the Colorado and Green River subbasins, Colorado and Utah. The historical population of Colorado Pikeminnows in the San Juan River of Colorado, New Mexico, and Utah was considered nearly extirpated (Tyus et al. 1982; Holden and Wick 1982; Platania

*Corresponding author: scott_durst@fws.gov
Received July 10, 2013; accepted November 14, 2013

et al. 1991), and efforts to augment this population via stocking mostly age-0, hatchery-reared fish has occurred annually since 1996. Young Colorado Pikeminnows are mostly insectivorous until they become large enough to consume fish prey at about 100 mm TL (Vanicek and Kramer 1969; Muth and Snyder 1995). Individuals larger than 200 mm TL can be entirely piscivorous (Vanicek and Kramer 1969). Females do not become reproductive until reaching 428–503 mm TL, typically at age 6 or older (Vanicek and Kramer 1969; Seethaler 1978). While augmentation efforts have increased the numbers of juvenile Colorado Pikeminnows in the San Juan River, stocked individuals are rarely encountered beyond 3 years poststocking, and the vast majority of individuals collected over the past decade consisted of juveniles, unlike the Colorado and Green River subbasins that also contained larger individuals.

Long-distance movements to complete life history requirements, such as spawning (Pellett et al. 1998; Paukert and Fisher 2001), have been extensively quantified in adult Colorado Pikeminnows (Tyus and McAda 1984; Tyus 1991; Modde and Irving 1998; Irving and Modde 2000). Apart from spawning migrations, adult Colorado Pikeminnows tend to occupy upstream habitats with higher prey densities but lower than optimal water temperatures, suggesting a balance between food and temperature preferences in these habitats (Osmundson et al. 1998). Following hatching, age-0 larvae drift downstream and settle in low-velocity habitats, where warmer temperatures may aid in fast growth and simultaneously limit intraspecific predation (Haynes et al. 1984; Bestgen et al. 2006). In the Colorado and Green River subbasins, juvenile Colorado Pikeminnows appear to be sedentary in downstream reaches within a single year but make long-distance upstream movements in subsequent years as they recruit into adult age-classes, possibly in response to higher prey densities in upstream reaches (Osmundson et al. 1998). Extensive study of Colorado Pikeminnows has accumulated much information on early and adult life stages, yet little is known about the life history of juveniles (i.e., age 1 to age 6). However, recent observations suggest juveniles can be highly mobile and use main-stem as well as small tributary habitats (Fresques et al. 2013).

Understanding the ontogenetic and ecological requirements of Colorado Pikeminnows should help inform recovery efforts in the Colorado River basin. We quantified seasonal movement and growth of juvenile Colorado Pikeminnows and associated spatial and temporal environmental variation to gain insights into the ecology of this life stage. Because the San Juan River is further south than other upper Colorado River basin rivers and the population in the San Juan River is derived almost exclusively from hatchery-reared fish, we also compared and contrasted life histories and length-at-age relationships of Colorado Pikeminnows in the San Juan River to previously published data on more natural populations elsewhere in the upper Colorado River basin.

METHODS

Study area.—The San Juan River originates in southwest Colorado and is a major tributary to the Colorado River, draining 99,200 km^2 in Arizona, Colorado, New Mexico, and Utah (Carlson and Carlson 1982). The completion of Navajo Dam in 1962 inundated 56 km of the river, which currently flows 365 km from Navajo Dam to Lake Powell (Figure 1). We used river kilometers (rkm) to designate locations along the San Juan River and considered rkm 0.0 at an impassable waterfall near the inflow to Lake Powell and rkm 365.0 the outlet of Navajo Dam. Fish community structure can vary longitudinally in the river (Ryden 2012; Gido and Propst 2012), probably due to differences in substrate, habitat availability, stream gradient, and water temperature (Bliesner and Lamarra 2002). The river exhibits some braiding upstream of rkm 107.2 but is mostly canyon-bound downstream of rkm 107.2.

Seasonal movement.—To quantify seasonal movement of juvenile Colorado Pikeminnows we relied on recaptures of individuals implanted with passive integrated transponder (PIT) tags between March and October of 2009–2012. We only investigated movement during those years because they had the highest number of Colorado Pikeminnow recaptures. During sampling trips designed to remove nonnative fishes and monitor large-bodied fishes, raft-mounted electrofishing (Smith-Root 5.0 GPP) units were used to collect fishes from rkm 289.7 to rkm 4.6. All Colorado Pikeminnows captured were scanned for PIT tags and measured (TL; mm), and their capture location (rkm) was recorded. Age-0 Colorado Pikeminnows originating from the hatchery-reared progeny of wild-collected adults were stocked each fall between 1996 and 2012 (yearly mean of 55 mm TL, range = 24–85 mm; Furr 2013), but individuals were not PIT-tagged until their first capture in the river one or more years poststocking. Only fish >150 mm TL were implanted with PIT tags, which were inserted into the peritoneal cavity medial to the pelvic fin.

Sampling varied both spatially and temporally over the 4 years, and some reaches of the river were sampled more intensely than others during each year. Because this spatial and temporal variation in sampling could influence observed patterns of movement, we only used data from sampling trips that occurred in close temporal proximity (1 week) covering the entire study area. These sampling trips occurred three times each year in spring (March–May), summer (June–August), and fall (September–October). Colorado Pikeminnow recaptures occurring outside of these combined riverwide seasonal sampling occasions were not included in movement analyses. To investigate seasonal movement, we quantified movement of individuals that were recaptured in spring and summer, summer and fall, or fall and spring. To investigate how size of individuals may influence movement, we correlated rates of movement (i.e., km/d to account for different numbers of days between recaptures) and lengths of individuals in each season with nonparametric

Downloaded by [US Fish & Wildlife Service] at 05:58 17 November 2015

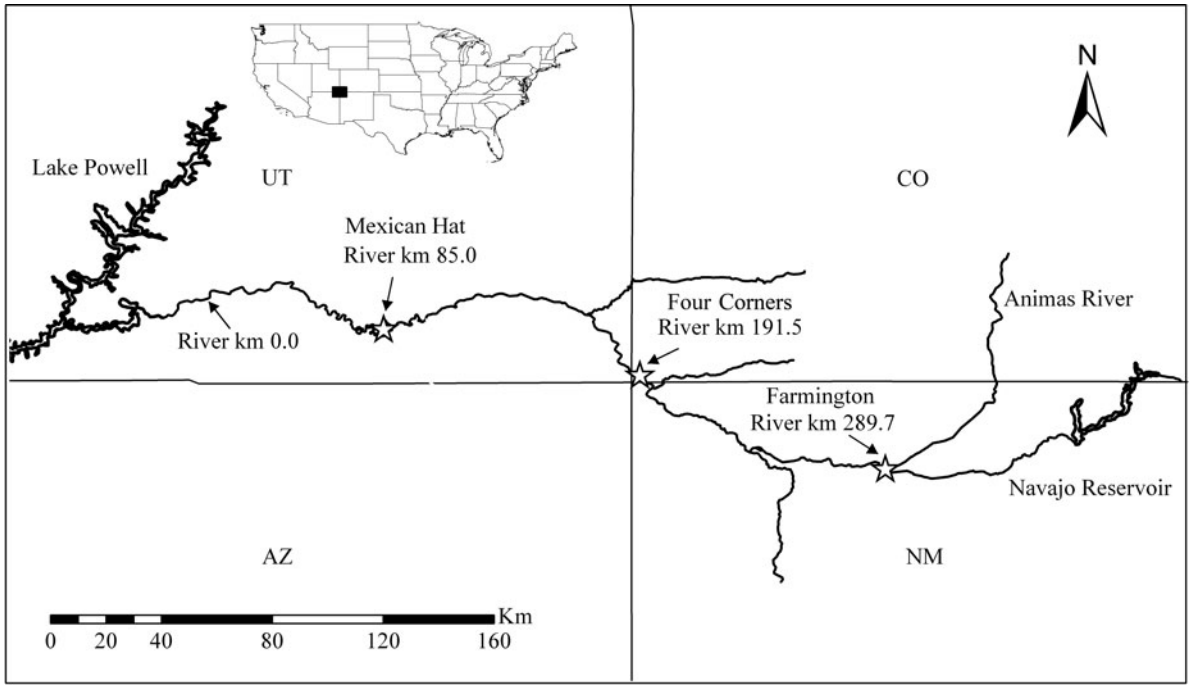

FIGURE 1. The San Juan River (NAD27) where movement and growth of Colorado Pikeminnows were assessed. The river flows from east to west and river kilometer (rkm) 107.2 is the beginning of canyon-bound reaches before the river enters Lake Powell. A waterfall that probably limits upstream movement of fishes is located near rkm 0.0 and Navajo Dam located at rkm 365 is a barrier to downstream and upstream movement. The star symbols indicate locations of temperature loggers.

Downloaded by [US Fish & Wildlife Service] at 05:58 17 November 2015

Spearman rank correlations. We only analyzed individuals that were collected at least 30 d apart. We did not assess annual variation in movement patterns due to low among year sample size.

To corroborate observed seasonal movement patterns, we assessed spatial variation in densities of Colorado Pikeminnows in fall and spring. We quantified CPUE (fish/h) from all sampling that occurred in the river between 2009 and 2012. We calculated mean Colorado Pikeminnow CPUE in five 48-km reaches from rkm 274–32 and used a general linear model (GLM) with $\log_{10}(x + 1)$-transformed CPUE as the dependent variable and season, rkm, and their interaction as fixed factors. A significant interaction would indicate that the spatial densities of Colorado Pikeminnows varied between fall and spring. For all GLM analyses we retained the interaction in the final model only if it was significant. Effect sizes for GLM analyses were estimated by use of partial eta^2 ($\eta_p{}^2$; the proportion of variance accounted for by each term in the model).

Spatial and temporal environmental variation.—We quantified spatial and temporal variation in water temperature to assess how this factor may have influenced seasonal movement of Colorado Pikeminnows (Siebert 1980; Osmundson et al. 1998). We calculated weekly mean water temperature at three locations during the entire year between 2003 and 2012 (Farmington, Four Corners, and Mexican Hat; Figure 1). Temperature was collected using Onset Corporation HOBO water temperature loggers that recorded data every 15 min. Temperature data were downloaded and checked for errors two to four times per year. Although we investigated movement only between 2009 and 2012, we included temperature data from 2003 to 2012 because we captured fish that were at least age-6 (see next section). We also obtained temperature data between 2003 and 2012 in the Colorado River (USGS gauge station 09163500 – Colorado River near Colorado–Utah state line) and Green River (USGS gauge station 09261000, Green River near Jensen, Utah) to compare the thermal regime of the San Juan River to rivers in the Upper Colorado River basin.

Colorado Pikeminnow growth.—We quantified seasonal growth rate as the change in TL over time (i.e., mm/d) for individuals that were captured at least twice during the same season (i.e., spring, summer, or fall) but at least 30 d apart from 2009 through 2012. Individuals were placed into one of six size classes (<175, 176–200, 201–250, 251–300, 301–350, and >351 mm TL). To assess how season and size of individuals influenced growth rates, we used a GLM with growth rate as the dependent variable and Season, Size class, and their interaction as fixed factors.

We quantified ontogenetic growth of Colorado Pikeminnows by comparing TL of individuals with their known age between 1997 and 2012. Because assigning Colorado Pikeminnows an age based on their size at capture was difficult, we only included individuals that were initially captured in their first year following stocking when they could be reliably assigned as age-1. To compare length-at-age of Colorado Pikeminnows in the San Juan River to those in the Colorado, White, Yampa, and Green

Downloaded by [US Fish & Wildlife Service] at 05:58 17 November 2015

rivers, we used our recapture data and scale-estimated length-at-age data from Hawkins (1992). All statistical analyses were conducted using PASW statistics v. 18.0.

RESULTS

Seasonal Movement

A total of 704 Colorado Pikeminnows were collected between 2009 and 2012; however, only 81 individuals were recaptured in successive seasons. Thirty-one individuals were captured in the spring and recaptured in the summer, and of those, 71% moved upstream a mean distance of 62.2 km (SD = 47.6; Figure 2). The remaining 29% moved downstream from spring to summer, but downstream movements were substantially shorter than upstream (mean = 4.7 km, SD = 4.6). Summer to fall movement was documented for 29 individuals, and direction of movement was more evenly distributed than spring to summer movements (moving upstream = 34%, downstream = 38%, and no movement = 28%). Upstream movements averaged 4.8 km (SD = 6.2), while downstream movements averaged 24.8 km (SD = 23.8). Movements over winter (fall to spring) were downstream for 18 individuals captured in fall and recaptured the next spring (mean = 35.2 km, SD = 43.7), and 3 individuals showed no overwinter movement.

When assessing relationships between the size of Colorado Pikeminnows and seasonal movement rates, we found only one significant relationship (Figure 3). In spring to summer movements, the length of Colorado Pikeminnows was positively correlated with rate of movement ($n = 31$, $r = 0.459$, $P = 0.009$), but no relationships were found in the summer to fall and fall to spring movements (both $P > 0.44$).

When assessing seasonal and spatial variation in Colorado Pikeminnow densities using a GLM, only rkm and the season × rkm interaction had significant effects (Table 1). The significant season × rkm interaction indicated densities varied spatially between seasons. Densities tended to be higher in upstream reaches during fall, but were higher in the lower reaches during spring (Figure 4).

TABLE 1. Results from general linear models assessing variation in Colorado Pikeminnow densities and growth rates in the San Juan River. Effects of variation in density were assessed by season and river kilometer, and variation in growth rate was assessed by season and size-class. The interaction between fixed factors was examined for each dependent variable, but only significant interactions were retained in the final model.

Dependent variable	Fixed factors	$F_{(df)}$	P	η_p^2
Density	Season	$3.27_{(1, 27)}$	0.082	0.108
	River kilometer	$2.79_{(4, 27)}$	0.047	0.292
	Season × river kilometer	$4.59_{(4, 27)}$	0.006	0.405
Growth rate	Season	$55.85_{(2, 565)}$	<0.001	0.165
	Size-class	$3.25_{(5, 565)}$	0.007	0.028

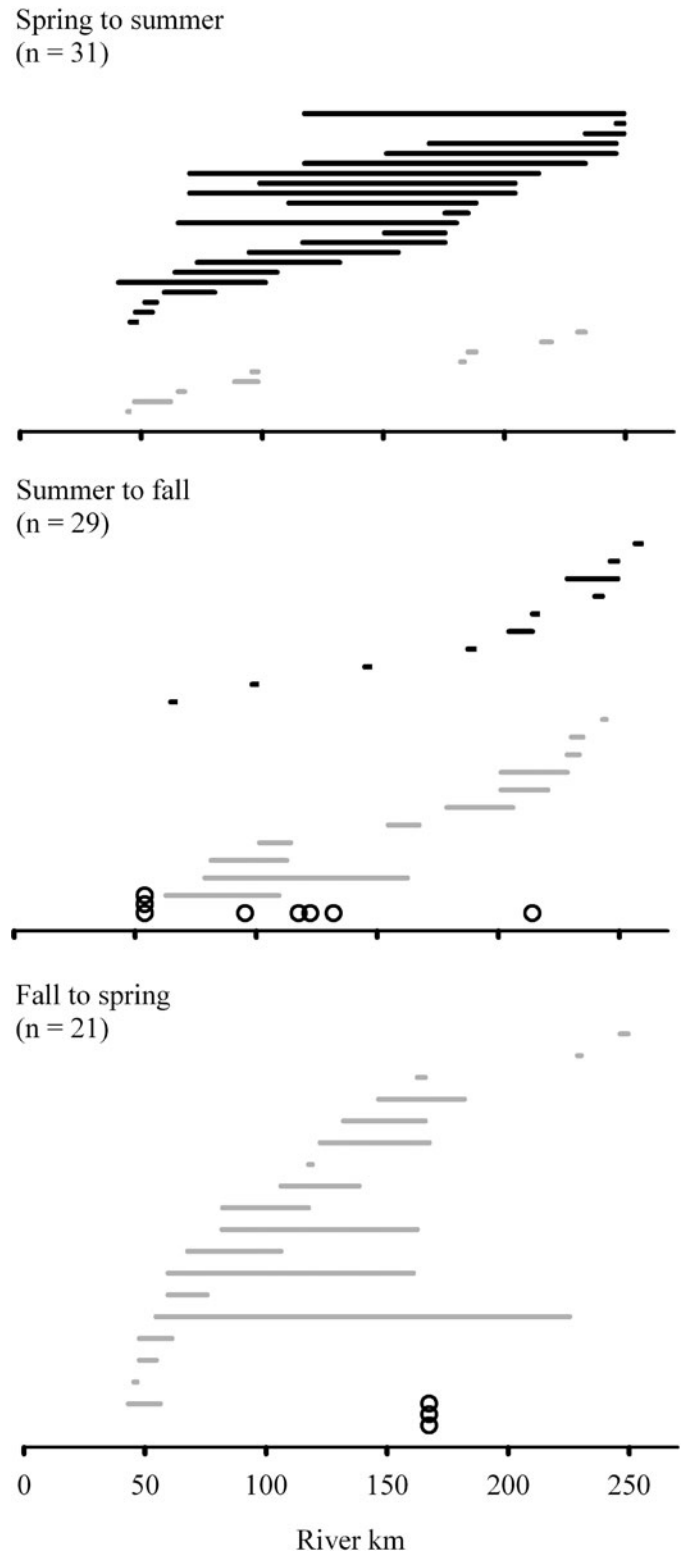

FIGURE 2. Seasonal movement patterns of Colorado Pikeminnows in the San Juan River between 2009 and 2012. Individuals tagged with passive integrated transponder tags and recaptured in consecutive seasons moved either upstream of release (black lines), downstream (gray lines), or did not change location (open circles). Bar lengths represent movement distances; i.e., the ends of each bar indicate the two capture locations.

Downloaded by [US Fish & Wildlife Service] at 05:58 17 November 2015

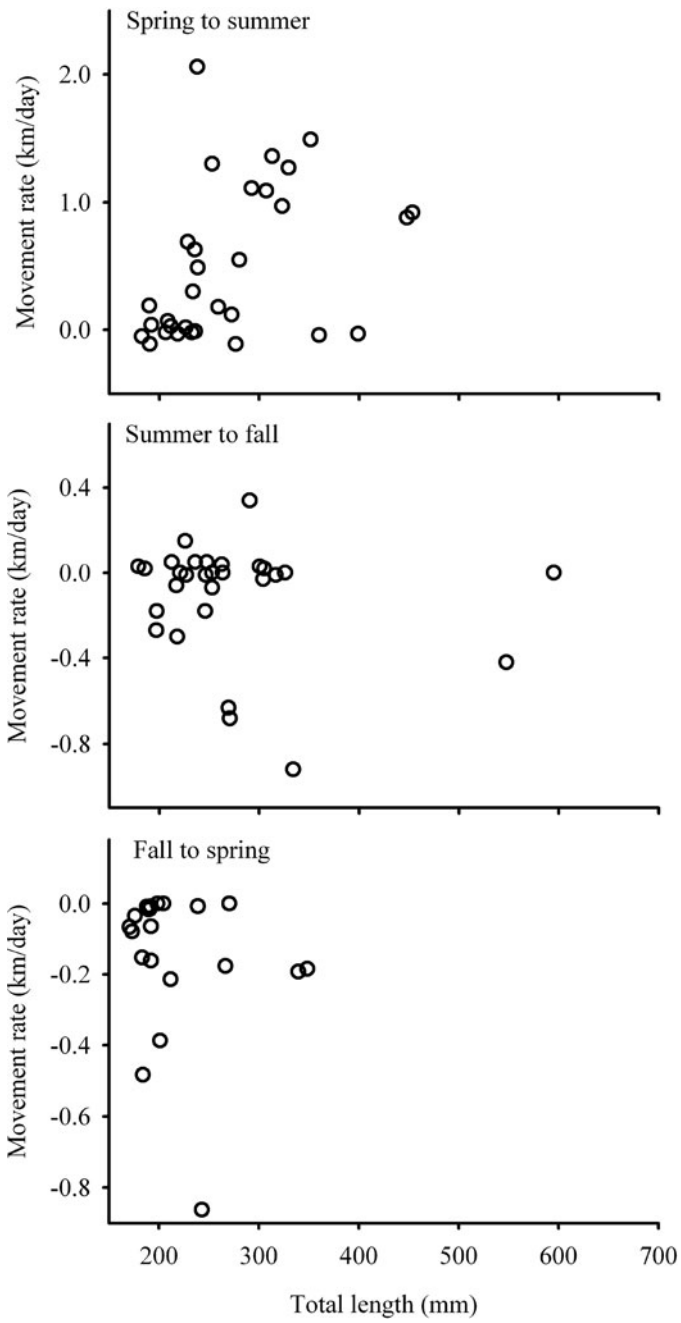

FIGURE 3. Relationship between rate of movement and total length of Colorado Pikeminnows in the San Juan River for spring to summer, summer to fall, and fall to spring (over winter) movements.

Spatial and Temporal Environmental Variation

Between 2003 and 2012, mean weekly temperatures in the San Juan River ranged from 1.6°C to 26.5°C and demonstrated substantial seasonal variation (Figure 5). Water temperature was higher at downstream sites during summer months, but all sites showed similarly low temperatures during winter. In addition, downstream reaches of the river tended to warm sooner in the spring than did upper reaches. Temperatures in the Colorado River and Green River were consistently lower than the San Juan River for most of the year, except in the most upstream location (i.e., Farmington; Figure 5).

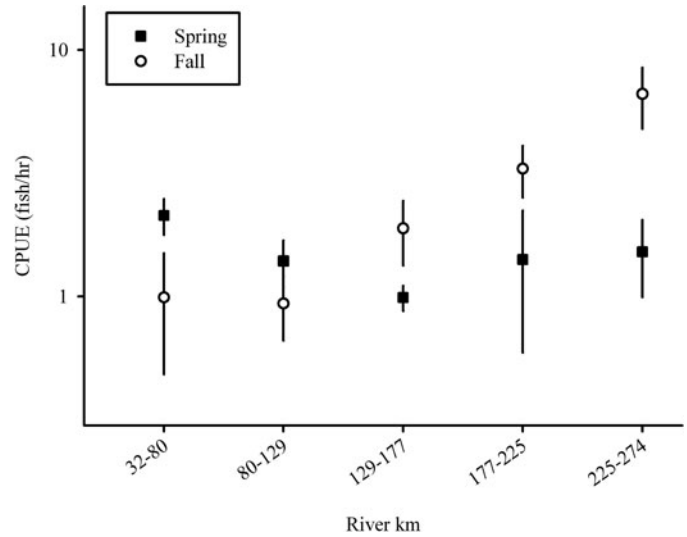

FIGURE 4. Mean (±1 SE) CPUE of Colorado Pikeminnows in the San Juan River during spring and fall between 2009 and 2012 by 48-km reaches. Note the *y*-axis is $\log_{10}$ scale.

Colorado Pikeminnow Growth

A total of 573 Colorado Pikeminnows were captured twice during the same season. We found season and size-class affected growth rate but season had a stronger effect than size-class with no significant season × size-class interaction (Table 1). Mean growth rates ranged from 0.06 to 0.60 mm/d, and growth was

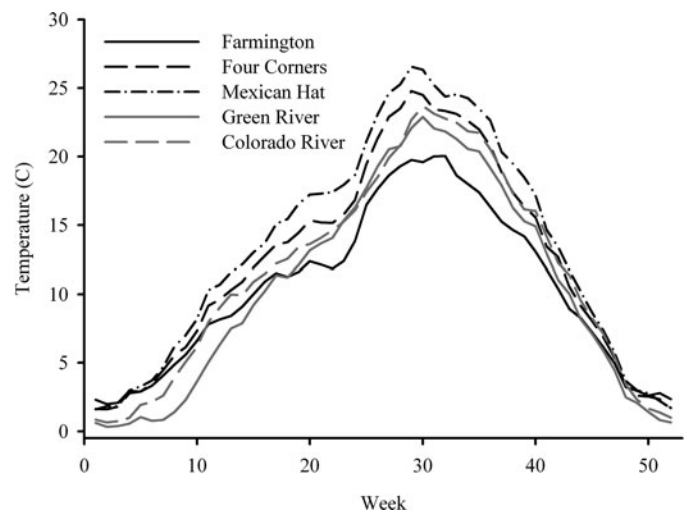

FIGURE 5. Mean weekly water temperature from three sites on the San Juan River and two sites in the upper Colorado River basin between 2003 and 2012. San Juan River sites were Farmington (rkm 289.7), Four Corners (rkm 191.5), and Mexican Hat (rkm 85.0). Temperature data were obtained from U.S. Geological Survey gauge station 09163500 in the Colorado River and from gauge station 09261000 in the Green River.

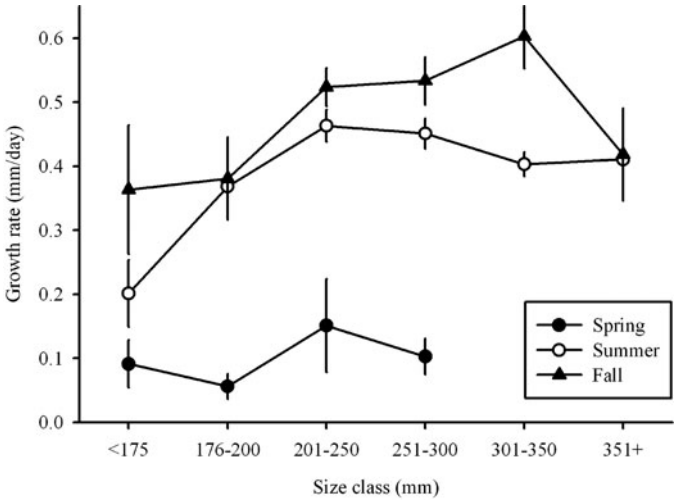

FIGURE 6. Mean (±1 SE) seasonal growth rate of Colorado Pikeminnows by size-class in the San Juan River during spring, summer, and fall between 2009 and 2012.

higher during summer and fall than spring (Figure 6). In addition, growth rates in the smallest two size-classes were generally lower than the larger size-classes.

There were 505 individuals initially captured as age 1 and subsequently recaptured that were used to quantify length-at-age relationships in the San Juan River. Age-1 individuals averaged 177 mm TL, while the oldest individual was age 6 and measured 550 mm TL (Figure 7). Length at age generally showed a linear pattern, and individuals in the San Juan River were consistently larger than fish of the same age from the Colorado, Green, White, and Yampa rivers.

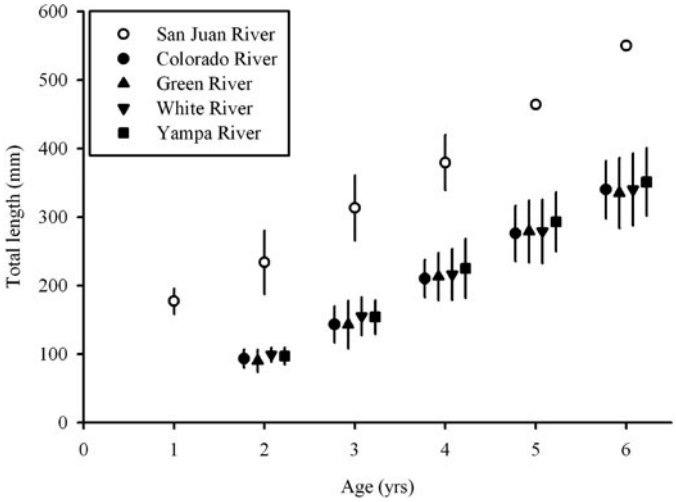

FIGURE 7. Mean (±1 SD) total length of Colorado Pikeminnows of known ages from the San Juan River, based on recapture data between 2009 and 2012 and length at age based on scale data from the Colorado, White, Green, and Yampa rivers (from Hawkins 1992).

DISCUSSION

Juvenile Colorado Pikeminnows moved upstream from spring to summer and downstream over winter. Higher catch rates in upstream reaches during fall and downstream during spring corroborated seasonal movement patterns. Rates of movement from spring to summer were also positively correlated with length of individuals. These seasonal and size-related movements may be linked to reproduction; however, few of these individuals were possibly of reproductive length (i.e., >428 mm TL). Most reproductive adults in the Colorado and Green rivers move downstream to specific spawning habitats after spring runoff and then return to upstream reaches (Tyus and McAda 1984; Tyus 1985), movements thought to be related to trade-offs between lower water temperatures and higher prey densities in upper reaches (Osmundson et al. 1998). On the other hand, adult Sacramento Pikeminnows *P. grandis*, a smaller relative of Colorado Pikeminnow, as well as other large-bodied cyprinids (Lucas and Batley 1996) move upstream during spring to find suitable spawning habitat and downstream overwinter because of habitat and metabolic limitations (Harvey and Nakamoto 1999). However, how environmental factors contribute to movement patterns of juvenile Colorado Pikeminnows is largely unknown.

Spatial and temporal variation in temperature and prey density may have contributed to observed movement patterns of juvenile Colorado Pikeminnows in the San Juan River. Longitudinal water temperature was similar during winter months, but lower reaches warmed sooner in spring and remained warmer during summer months than did upper reaches, a pattern probably ubiquitous in most river systems (Zwieniecki and Newton 1999; Torgersen et al. 2001; Cassie 2006). Seasonal fish movements between canyon-bound and noncanyon reaches of Aravaipa Creek, Arizona, were presumably in response to favorable temperature regimes (Siebert 1980). We speculate that downstream movement of juvenile Colorado Pikeminnows during winter may be a strategy that would extend the growing season as opposed to staying in upper reaches during winter and into spring. Fast growth to overcome gape-limitation can be particularly important for recruitment of piscivorous fishes (Persson and Brönmark 2002); relative gape limitations are lower in smaller Colorado Pikeminnows (Burnette and Gibb 2013), making a strategy of maximizing growth by following predictable spatial temperature regimes advantageous. Yet, prey densities can also influence the spatial distribution of Colorado Pikeminnows (Osmundson et al. 1998; Franssen and Durst, in press). Thus, juvenile Colorado Pikeminnows potentially balance favorable temperatures with prey availability in their seasonal and longitudinal distribution. Although small-bodied prey species and juvenile Colorado Pikeminnows tend to be more abundant in upstream reaches during fall (Franssen and Durst, in press), seasonal variation in longitudinal prey density is unknown. Because the Colorado Pikeminnow population in the San Juan River consists almost entirely of hatchery-reared fish, these seasonal movement patterns will need to be investigated

Downloaded by [US Fish & Wildlife Service] at 05:58 17 November 2015

Downloaded by [US Fish & Wildlife Service] at 05:58 17 November 2015

in natural populations to assess their ubiquity because hatchery-reared fish may not exhibit the same behavior as wild conspecifics (Irving and Modde 2000).

Understanding seasonal movement of different life stages of Colorado Pikeminnows will be essential for population recovery, but movement may be particularly important in systems with impassable barriers. To facilitate their retention in the San Juan River, age-0 Colorado Pikeminnows are stocked upstream of most impassable or selective fish weirs; these barriers may impede only upstream movement, although most, if not all, barriers are probably passable during high water. However, since 2002 a large and probably impassable waterfall has persisted near the San Juan River's confluence with Lake Powell (rkm 0.0). Thus, any Colorado Pikeminnows moving over the waterfall may be precluded from returning to the river proper. Observational data on the limited persistence of individual Colorado Pikeminnows (i.e., fish are rarely encountered >3 years after stocking) and the strong downstream movement of individuals during winter suggests the waterfall may be an impediment to population recovery in the San Juan River due to net emigration. In fact, both juvenile and adult Colorado Pikeminnows that originated from stockings into the San Juan River were collected below the waterfall in Lake Powell during fish surveys in 2011 (Francis et al. 2013).

Length-at-age relationships indicated Colorado Pikeminnows in the San Juan River were larger than fish of the same age from other populations in the Colorado River basin. While the thermal regimes observed in most of the San Juan River were warmer than those in the Colorado and Green rivers and could have resulted in higher growth rates, age-0 hatchery fish stocked into the San Juan River each fall were likely larger than wild-spawned individuals of the same age in the upper Colorado River (Vanicek and Kramer 1969; Osmundson et al. 1997). Despite the larger length at age observed in the San Juan River, it is not known if these fish reach reproductive maturity at an earlier age than those in other upper Colorado River basin populations.

In the San Juan River seasonal variation in growth rates suggests warmer temperatures contributed to faster growth; fish grew faster in summer and fall than in spring. Although faster growth among all size-classes in warmer seasons was predictable, slower growth rates in fish <200 mm TL was surprising. Fish usually exhibit fastest growth as young individuals, and growth slows when they reach sexual maturity (Ricker 1975; Chen et al. 1992), a pattern demonstrated in other Colorado Pikeminnow populations (Osmundson et al. 1997; Osmundson 2006) as well as other piscivores (Olson 1996). It is unclear why smaller Colorado Pikeminnows in the San Juan River have slower growth rates than larger individuals. Although possible, it does not appear that insertion of PIT tags has negative effects on growth and survival for even small individuals of other fishes (Peterson et al. 1994; Acolas et al. 2007). Increasing growth rates may be particularly important for reducing mortality of young-of-year and juvenile fish because larger Colorado Pikeminnows tend to show higher overwinter survival (Thompson et al. 1991). Prey densities can also have strong impacts on growth in piscivorous fishes (Fox 1989; Olson 1996; Graeb et al. 2004), suggesting prey limitation could be responsible for slower growth rates of smaller Colorado Pikeminnows in the San Juan River. Franssen et al. (2007) suggested small Colorado Pikeminnows may be prey restricted due to gape limitations during critical periods of summer growth. In addition, Colorado Pikeminnows in these smaller size-classes are likely undergoing an ontogenetic diet shift from invertebrates to fish prey (Vanicek and Kramer 1969); therefore, invertebrate prey limitations could also contribute to slower growth. These slow growth rates may represent a bottleneck and contribute to the low recruitment success in the San Juan River. Alternatively, the limited recruitment of Colorado Pikeminnows in the San Juan River could be related to increased predation susceptibility, or reduced survival due to their hatchery-reared origin (Irving and Modde 2000; Araki and Schmid 2010). A detailed assessment of spatial and temporal variation in potential prey of small Colorado Pikeminnows would be useful to elucidate possible mechanisms behind the observed slower growth rates.

Selective pressures have shaped the life histories of Colorado Pikeminnows over its evolutionary history in the Colorado River basin, yet contemporary anthropogenic environmental change has reduced its range, altered flow and temperature regimes, and contributed to the establishment of nonnative species. Releases of hypolimnetic water from Navajo Dam and the physical barrier of the dam itself prevent Colorado Pikeminnows from recolonizing historically occupied upstream reaches, while the waterfall limits the return of individuals lost from the San Juan River to Lake Powell. Thus, the length of the San Juan River in which to recover Colorado Pikeminnows is considerably reduced. Additionally, a naturally reproducing and recruiting population of Colorado Pikeminnows derived from hatchery-reared augmentation efforts may be impeded by prey limitations in the San Juan River. Determining how life history traits of Colorado Pikeminnows interact with the human-modified Colorado River basin will be requisite to developing strategies for its recovery throughout the basin.

ACKNOWLEDGMENTS

We thank the staff from the U.S. Fish and Wildlife Service's Colorado River Fishery Project, Grand Junction, Colorado; U.S. Fish and Wildlife Service's New Mexico Fish and Wildlife Conservation Office, Albuquerque, New Mexico; Utah Division of Wildlife Resources, Moab, Utah; Navajo Nation Department of Fish and Wildlife, Window Rock, Arizona; Miller Ecological Consultants, Fort Collins, Colorado; and Keller–Bliesner Engineering, Logan, Utah, for their assistance and dedication that made this project possible. Funding for this work was provided through authorizing legislation for the San Juan River Basin Recovery Implementation Program administered by U.S. Bureau of Reclamation, Salt Lake City, Utah. This article reflects the

views of the authors and does not necessarily reflect the view of the U.S. Fish and Wildlife Service. Reference to trade names does not imply endorsement by the U.S. Government. We thank K. Gido, D. Propst, T. Turner, and M. Dela Cruz for thoughtful comments that greatly improved the manuscript.

REFERENCES

Acolas, M. L., J. M. Roussel, J. M. Lebel, and J. L. Banliniére. 2007. Laboratory experiment on survival, growth and tag retention following PIT injection into the body cavity of juvenile Brown Trout (*Salmo trutta*). Fisheries Research 86:280–284.

Araki, H., and C. Schmid. 2010. Is hatchery stocking a help or harm? Evidence, limitations and future directions in ecological and genetic surveys. Aquaculture 308:S1–S11.

Bestgen, K. R., D. W. Beyers, J. A. Rice, and G. B. Haines. 2006. Factors affecting recruitment of young Colorado Pikeminnow: synthesis of predation experiments, field studies, and individual-based modeling. Transactions of the American Fisheries Society 135:1722–1742.

Bliesner, R., and V. Lamarra. 2000. Hydrology, geomorphology, and habitat studies. Keller–Bliesner Engineering and Ecosystems Research Institute, Report to San Juan River Basin Recovery Implementation Program, Logan, Utah.

Burnette, M. F., and A. C. Gibb. 2013. Do changes in morphology and prey-capture movements facilitate a dietary transition in juvenile Colorado Pikeminnow, *Ptychocheilus lucius*? Evolutionary Biology 40:251–275.

Carlson, C. A., and E. M. Carlson. 1982. Review of selected literature on the upper Colorado River system and its fishes. Pages 1–8 *in* W. H. Miller, H. M. Tyus, C. A. Carlson, editors. Fishes of the upper Colorado River system: present and future. American Fisheries Society, Western Division, Bethesda, Maryland.

Cassie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51:1389–1406.

Chen, Y., D. A. Jackson, and H. H. Harvey. 1992. A comparison of von Bertalanffy and polynomial functions in modeling fish growth data. Canadian Journal of Fisheries and Aquatic Sciences 49:1228–1235.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441–451.

Fox, M. G. 1989. Effect of prey density and prey size on growth and survival of juvenile Walleye (*Stizostedion vitreum vitreum*). Canadian Journal of Fisheries and Aquatic Sciences 46:1323–1328.

Francis, T. A., D. W. Ryden, B. J. Schleicher, and D. S. Elverud. 2013. San Juan River arm of Lake Powell Razorback Sucker (*Xyrauchen texanus*) survey: 2011. U.S. Bureau of Reclamation, Agreements R11 PG 40 0009 and R11 AP 40 004, Final Interim Progress Report, Salt Lake City.

Franssen, N. R., and S. L. Durst. In press. Prey and nonnative fish predict the distribution of Colorado Pikeminnow (*Ptychocheilus lucius*) in a south-western river in North America. Ecology of Freshwater Fish. DOI: 10.1111/eff.12093.

Franssen, N. R., K. B. Gido, and D. L. Propst. 2007. Flow regime affects availability of nonnative prey of an endangered predator. Biological Conservation 138:330–340.

Fresques, T. D., R. C. Ramey, and G. J. Dekleva. 2013. Use of small tributary streams by subadult Colorado Pikeminnow (*Ptychocheilus lucius*) in Yellow Jacket Canyon, Colorado. Southwestern Naturalist 58:104–107.

Furr, D. W. 2013. Augmentation of Colorado Pikeminnow (*Ptychocheilus lucius*) in the San Juan River 2012. U.S. Fish and Wildlife Service, San Juan River Basin Recovery Implementation Program, Albuquerque, New Mexico.

Gido, K. B., and D. L. Propst. 2012. Long-term dynamics of native and nonnative fishes in the San Juan River, New Mexico and Utah under a partially managed flow regime. Transactions of the American Fisheries Society 141:645–659.

Gowan, C., and K. D. Fausch. 2002. Why do foraging stream salmonids move during summer? Environmental Biology of Fishes 64:139–153.

Graeb, B. D., J. M. Dettmers, D. H. Wahl, and C. E. Cáceres. 2004. Fish size and prey availability affect growth, survival, prey selection, and foraging behavior of larval Yellow Perch. Transactions of the American Fisheries Society 133:504–514.

Harvey, B. C. 1991. Interactions among stream fishes: predator-induced habitat shifts and larval survival. Oecologia 87:29–36.

Harvey, B. C., and R. J. Nakamoto. 1999. Diel and seasonal movements by adult Sacramento Pikeminnow (*Ptychocheilus grandis*) in the Eel River, northwestern California. Ecology of Freshwater Fish 8:209–215.

Hawkins, J. A. 1992. Age and growth of Colorado Squawfish from the upper Colorado River basin, 1978–1990. Master's thesis. Colorado State University, Fort Collins.

Haynes, C. M., T. A. Lytle, E. J. Wick, and R. T. Muth. 1984. Larval Colorado Squawfish (*Ptychocheilus lucius* Girard) in the upper Colorado River basin, Colorado, 1979–1981. Southwestern Naturalist 29:21–33.

Holden, P. B., and E. J. Wick. 1982. Life history and prospects for recovery of Colorado Squawfish. Pages 98–108 *in* W. H. Miller, H. M. Tyus, C. A. Carlson, editors. Fishes of the upper Colorado River system: present and future. American Fisheries Society, Western Division, Bethesda, Maryland.

Hughes, N. F. 1992. Ranking of feeding positions by drift-feeding Arctic Grayling (*Thymallus arcticus*) in dominance hierarchies. Canadian Journal of Fisheries and Aquatic Sciences 49:1994–1998.

Hughes, N. F. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology 79:281–294.

Irving, D. B., and T. Modde. 2000. Home-range fidelity and use of historic habitat by adult Colorado Pikeminnow (*Ptychocheilus lucius*) in the White River, Colorado and Utah. Western North American Naturalist 60:16–25.

Krivan V. 2003. Ideal free distributions when resources undergo population dynamics. Theoretical Population Biology 64:25–38.

Lucas, M. C., and E. Batley. 1996. Seasonal movements and behavior of adult Barbell *Barbus barbus*, a riverine cyprinid fish: implications for river management. Journal of Applied Ecology 33:1345–1358.

Magoulick, D. D. 2004. Effects of predation risk on habitat selection by water column fish, benthic fish and crayfish in stream pools. Hydrobiologia 527:209–221.

Modde, T., and D. B. Irving. 1998. Use of multiple spawning sites and seasonal movement by Razorback Suckers in the middle Green River, Utah. North American Journal of Fisheries Management 18:318–326.

Montgomery, W. I., W. L. Wilson, R. Hamilton, and P. McCartney. 1991. Dispersion in the Wood Mouse, *Apodemus sylvaticus*—variable resources in time and space. Journal of Animal Ecology 60:179–192.

Moody, A. L., A. I. Houston, and J. M. McNamara. 1996. Ideal free distributions under predation risk. Behavioral Ecology and Sociobiology 38:131–143.

Muth, R. T., and D. E. Snyder. 1995. Diets of young Colorado Squawfish and other small fish in backwaters of the Green River, Colorado and Utah. Great Basin Naturalist 55:95–104.

Olson, M. H. 1996. Ontogenetic niche shifts in Largemouth Bass: variability and consequences for first-year growth. Ecology 77:179–190.

Osmundson, D. B., R. J. Ryel, and T. E. Mourning. 1997. Growth and survival of Colorado Squawfish in the upper Colorado River. Transactions of the American Fisheries Society 126:687–698.

Osmundson, D. B., R. J. Ryel, M. E. Tucker, D. B. Burdick, and W. R. Elmblad. 1998. Dispersal patterns of subadult and adult Colorado Squawfish in the Upper Colorado River. Transactions of the American Fisheries Society 127:943–956.

Osmundson, D. B. 2006. Proximate causes of sexual size dimorphism in Colorado Pikeminnow, a long-lived cyprinid. Journal of Fish Biology 68:1563–1588.

Paukert, C. P., and W. L. Fisher. 2001. Spring movement of Paddlefish in a prairie reservoir system. Journal of Freshwater Ecology 16:113–124.

Pellett, T. D., G. J. Van Dyck, and J. V. Adams. 1998. Seasonal migration and homing of Channel Catfish in the lower Wisconsin River, Wisconsin. North American Journal of Fisheries Management 18:85–95.

Downloaded by [US Fish & Wildlife Service] at 05:58 17 November 2015

Persson, A., and C. Brönmark. 2002. Foraging capacity and resource synchronization in an ontogenetic diet switcher, Pikeperch (*Stizostedion lucioperca*). Ecology 83:3014–3022.

Peterson, N. L., E. F. Prentice, and T. P. Quinn. 1994. Comparison of sequential coded wire and passive integrated transponder tags for assessing overwinter growth and survival of juvenile Coho Salmon. North American Journal of Fisheries Management 14:870–873.

Platania, S. P., K. B. Bestgen, M. A. Moretti, D. L. Propst, and J. E. Brooks. 1991. Status of Colorado Squawfish and Razorback Sucker in the San Juan River, Colorado, New Mexico, and Utah. Southwestern Naturalist 36:147–150.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Ryden, D. W. 2012. Long term monitoring of sub-adult and adult large-bodied fishes in the San Juan River: 2010. U.S. Bureau of Reclamation, Agreement 08-AA-40-2715, Final Interim Progress Report, Salt Lake City.

Seethaler, K. H. 1978. Life history and ecology of Colorado Squawfish (*Ptychocheilus lucius*) in the upper Colorado River basin. Master's thesis. Utah State University, Logan.

Siebert, D. J. 1980. Movements of fishes in Aravaipa Creek, Arizona. Doctoral dissertation. Arizona State University, Tempe.

Thompson, J. M., E. P. Bergersen, C. A. Carlson, and L. R. Kaeding. 1991. Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado Squawfish. Transactions of the American Fisheries Society 120:346–353.

Torgersen, C. E., R. N. Faux, B. A. McIntosh, N. J. Poage, and D. J. Norton. 2001. Airborne thermal sensing for water temperature assessment in rivers and streams. Remote Sensing of Environment 76:386–398.

Tyler, J. A., and K. A. Rose. 1994. Individual variability and spatial heterogeneity in fish population models. Reviews in Fish Biology and Fisheries 4:91–123.

Tyus, H. M. 1985. Homing behavior noted for Colorado Squawfish. Copeia 1985:213–215.

Tyus, H. M. 1991. Ecology and management of Colorado Squawfish. Pages 379–402 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson.

Tyus, H. M., B. D. Burdick, R. A. Valdez, C. M. Haynes, T. A. Lytle, and C. R. Berry. 1982. Fishes of the upper Colorado River basin: distribution, abundance, and status. Pages 12–70 *in* W. H. Miller, H. M. Tyus, and C. A. Carlson, editors. Fishes of the upper Colorado River system: present and future. American Fisheries Society, Western Division, Bethesda, Maryland.

Tyus, H. M., and C. W. McAda. 1984. Migration, movements and habitat preferences of Colorado Squawfish, *Ptychocheilus lucius*, in the Green, White and Yampa rivers, Colorado and Utah. Southwestern Naturalist 29:289–299.

USFWS (U.S. Fish and Wildlife Service). 1967. Native fish and wildlife: endangered species. Federal Register 32(11 March 1967):48:4001.

Vanicek, D. C., and R. H. Kramer. 1969. Life history of the Colorado Squawfish, *Ptychocheilus lucius*, and the Colorado Chub, *Gila robusta*, in the Green River in Dinosaur National Monument, 1964–1966. Transactions of the American Fisheries Society 98:193–208.

Ward, A. J. W., M. M. Webster, and P. J. B. Hart. 2006. Intraspecific food competition in fishes. Fish and Fisheries 7:231–261.

Zwieniecki, M. A., and M. Newton. 1999. Influence of streamside cover and stream features on temperature trends in forested streams of Western Oregon. Western Journal of Applied Forestry 14:106–113.

Downloaded by [US Fish & Wildlife Service] at 05:58 17 November 2015