Population Characteristics and the Influence of Discharge on Bluehead Sucker and Flannelmouth Sucker

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Rivers are among some of the most complex and important ecosystems in the world. Unfortunately, many fishes endemic to rivers have suffered declines in abundance and distribution suggesting that alterations to lotic environments have negatively influenced native fish populations. Of the 35 fishes native to the Colorado River basin (CRB), seven are considered either endangered, threatened, or species of special concern. As such, the conservation of fishes native to the CRB is a primary interest for natural resource management agencies. One of the major factors limiting the conservation and management of fishes endemic to the CRB is the lack of basic information on their ecology and population characteristics. We sought to describe the population dynamics and demographics of three populations of Bluehead Suckers (*Catostomus discobolus*) and Flannelmouth Suckers (*C. latipinnis*) in Utah. Additionally, we evaluated the potential influence of altered flow regimes on the recruitment and growth of Bluehead Suckers and Flannelmouth Suckers. Mortality of Bluehead Suckers and Flannelmouth Suckers from the Green, Strawberry, and White rivers was comparable to other populations. Growth of Bluehead Suckers and Flannelmouth Suckers was higher in the Green, Strawberry, and White rivers when compared to other populations in the CRB. Similarly, recruitment indices suggested that Bluehead Suckers and Flannelmouth Suckers in the Green, Strawberry, and White rivers had more stable recruitment than other populations in the CRB. Models relating growth and recruitment to hydrological indices provided little explanatory power. Notwithstanding, our results indicate that Bluehead Suckers and Flannelmouth Suckers in the Green, Strawberry, and White rivers represent fairly stable populations and provide baseline information that will be valuable for the effective management and conservation of the species.

RIVERS rank as one of the most diverse, complex, and important ecosystems in the world (Naiman et al., 1993). Rivers connect freshwater systems and are fundamental to the regulation and maintenance of terrestrial and aquatic environments (Dynesius and Nilsson, 1994). Unfortunately, lotic systems have undergone substantial anthropogenic alterations since the early 19th century (Mrowka, 1974; Baxter, 1977). For instance, only 40 rivers greater than 200 km in length remain free-flowing in the contiguous United States (Benke, 1990). The unrestrained manipulation of aquatic systems has resulted in extensive habitat degradation caused by sediment loading, pollution, flow and temperature alteration, impoundment, and channelization (Benke, 1990; Allan and Flecker, 1993; Poff et al., 1997; Richter et al., 1997). River modifications have, in turn, negatively influenced ecosystem function and freshwater fauna (Ricciardi and Rasmussen, 1999; Cooke et al., 2005). Rivers in arid regions are particularly susceptible to anthropogenic influences (Arthington and Balcombe, 2011) due to their characteristic extreme variability in discharge (Walker et al., 1995). Ichthyofauna in rivers in arid regions are specifically adapted to the harsh, unpredictable environment characteristic of arid-region rivers and are thus more vulnerable to changes to hydrologic regimes caused by flood control, impoundments, and water diversion (Young and Kingsford, 2006).

Fishes of the Colorado River basin (CRB) are perhaps one of the best examples of how human changes to hydrologic regimes can negatively influence fish populations in arid regions (Minckley and Deacon, 1968). Many fishes endemic to the CRB are uniquely evolved to survive the severe environment characteristics (e.g., erratic flows, variable temperatures, high salinity, high sediment loads) of the system (Bezzerides and Bestgen, 2002). "Big-river" fishes endemic to the CRB possess morphological features (e.g., streamlined bodies, keeled or humped dorsal surface, large, falcate fins) that improve swimming ability and stability in turbulent flows (Minckley et al., 1986; Minckley, 1991). Furthermore, native fishes of the CRB exhibit spawning seasons initiated by temperature and flow conditions (Stearns, 1977; Scoppettone, 1988). Dams and water diversions inundate lotic habitats and alter thermal and flow regimes (Collier et al., 1996), ultimately threatening native fishes adapted to the natural environmental conditions of the basin. Of the 35 species endemic to the CRB, seven (Bluehead Sucker [*Catostomus discobolus*], Bonytail [*Gila elegans*], Colorado Pikeminnow [*Ptychocheilus lucius*], Flannelmouth Sucker [*C. latipinnis*], Humpback Chub [*G. cypha*], Razorback Sucker [*Xyrauchen texanus*], Roundtail Chub [*G. robusta*]) are considered either endangered, threatened, or species of special concern (Bezzerides and Bestgen, 2002; Jelks et al., 2008). Efforts to restore and correct factors limiting Bonytail, Colorado Pikeminnow, Humpback Chub, and Razorback Sucker populations are ongoing (USFWS, 2002a, 2002b, 2002c). However, conservation efforts focused on Bluehead Suckers and Flannelmouth Suckers are limited by a lack of information on the basic population characteristics and ecology of the species.

Bluehead Suckers and Flannelmouth Suckers have drastically declined in abundance and distribution over the past century (Bezzerides and Bestgen, 2002). For example, Bezzerides and Bestgen (2002) estimated that both species now occupy approximately 45–50% of their historical distribution. As such, conservation of Bluehead Suckers and Flannelmouth Suckers is a primary management interest in regions where they occur. Unfortunately, relatively little

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Submitted: 23 November 2016. Accepted: 20 April 2017. Associate Editor: J. F. Schaefer.
© 2017 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CE-16-554 Published online: 7 July 2017

information on the basic population structure and function of the species is available. Improved understanding of the demographics (e.g., age structure) and dynamics (e.g., somatic growth) of Bluehead Suckers and Flannelmouth Suckers is critical for their effective management and conservation (Ricker, 1975). Population demographics and dynamics, especially information on recruitment, growth, and mortality, provide valuable insight on abiotic perturbations and the availability of resources (Guy and Brown, 2007; Allen and Hightower, 2010; Quist et al., 2012). For instance, Rowell et al. (2008) showed that diversions of the Colorado River reduced growth of juvenile Totoaba (*Totoaba macdonaldi*) by 50% and maturation by 1–5 years. The authors linked reductions in growth and maturity to the elimination of estuarine habitat in the Gulf of California. As basic population characteristics are lacking for both species throughout much of their distribution, we sought to describe the demographics and dynamics of three populations of Bluehead Suckers and Flannelmouth Suckers in northeastern Utah. In addition, we evaluated whether altered flow regimes were related to the growth and recruitment of both species.

MATERIALS AND METHODS

The Green River is the largest tributary of the Colorado River and drains portions of Wyoming, Utah, and Colorado (Fig. 1). Discharge in the Green River has been regulated by operation of Flaming Gorge Dam since 1963. Previous research suggests that the Utah portion of the Green River supports abundant, reproductively mature populations of Bluehead Suckers and Flannelmouth Suckers (Breen and Hedrick, 2009, 2012). The Strawberry River is a tributary of the Duchesne River (a tributary of the Green River), and is impounded by Soldier Creek and Starvation dams. Although the Strawberry River is isolated from large-river habitats, Bluehead Sucker and Flannelmouth Sucker populations appear to be fairly abundant as evidenced by high catch rates (Breen and Hedrick, 2009). The White River is the second largest tributary of the Green River and drains portions of Colorado and Utah. In 1984, Taylor Draw Dam was constructed on the White River creating Kenney Reservoir near Rangely, Colorado. When compared to the Green and Strawberry rivers, the White River has the highest catch rates of both species (Breen and Hedrick, 2009). Although altered by impoundments, the hydrographs of the Green, Strawberry, and White rivers exhibit fluctuations in discharge typical of arid-region rivers (Fig. 2). Snowmelt-runoff generally produces high-flow periods during the spring, whereas summer, autumn, and winter are typically low-flow periods (Bishop and Porcella, 1980). Although floodplain habitat has not been extensively surveyed in the Green, White, and Strawberry rivers, each system connects to off-channel habitats at high flows. For example, Valdez and Nelson (2004) suggested annual flows greater than or equal to 235 m^3/s would inundate off-channel habitats in the upper Green River and likely benefit recruitment of Colorado Pikeminnow. Similarly, Webber et al. (2013) noted that a high-flow event (141 m^3/s) in the spring of 2011 inundated off-channel habitats and created backwaters in the White River. The Strawberry River has limited floodplain interaction until the river nears Starvation Reservoir.

As part of a larger fish monitoring program in Utah, Bluehead Suckers and Flannelmouth Suckers were sampled from portions of the Green, Strawberry, and White rivers. In the Green River, sampling was conducted in three river sections in the spring and summer of 2009–2011 (Section 1 [length = 20 km], Section 2 [117.8 km], Section 3 [184 km]; Fig. 1). Four 200 m reaches were sampled on the Strawberry River between Strawberry and Starvation reservoirs (Fig. 1). The Strawberry River was sampled in June of 2009 and September of 2010. The White River was sampled downstream from the Colorado–Utah border for approximately 68 km in the spring and summer of 2009–2011 (Fig. 1).

Bluehead Suckers and Flannelmouth Suckers were collected using pulsed-DC electrofishing. Depending on habitat type (e.g., rapids), fish were sampled with boat, cataraft, or barge electrofishing systems. Electrofishing boats and catarafts were equipped with a 5.0 GPP Electrofisher (Smith-Root, Inc., Vancouver, Washington). The electrofishing barge was equipped with a 1.5 KVA Electrofisher (Smith-Root, Inc., Vancouver, WA). Boats and catarafts sampled along each shoreline of a given reach in a single, downstream pass. Reaches sampled with the electrofishing barge were sampled in their entirety in a single, upstream pass.

Sampled fishes were measured to the nearest millimeter (total length) and weighed to the nearest gram. Marginal pectoral-fin rays were removed by cutting immediately proximal to the insertion of the fin ray (Koch and Quist, 2007; Quist et al., 2007). Following measurement and pectoral-fin ray removal, fish were returned to the water. Pectoral-fin rays were stored in individually labeled coin envelopes and sent to the University of Idaho for age and growth analysis. After drying, fin rays were mounted in epoxy following methods described by Koch and Quist (2007) and cut into 0.8 mm thick sections using a low-speed Isomet saw (Buehler, Inc., Lake Bluff, IL). Cross-sections were examined using a dissecting microscope with transmitted light and an image analysis system (Image-Pro Plus; Media Cybernetics, Silver Spring, MD). Annuli were enumerated independently by two readers without knowledge of fish length and sampling location. Both readers had experience enumerating annuli of various structures prior to the study. After each reader assigned an age, age estimates were compared. If discrepancies existed between age estimates, the structure was re-aged by both readers and discussed in a mutual reading.

Data were analyzed by species and river. The Green River was further separated into upper (upstream of the White River confluence) and lower (downstream of White River confluence) sections to account for changes in geomorphology and tributary inputs. An age-length key was used to estimate the age distribution of Bluehead Suckers and Flannelmouth Suckers in a given river system (Isely and Grabowski, 2007; Quist et al., 2012). Total annual mortality (A) was estimated using a Chapman-Robson estimator with a peak-plus criterion (Chapman and Robson, 1960; Smith et al., 2012). Recruitment was described using the residual technique (Maceina, 1997) to better understand year-class strength, and the recruitment coefficient of determination (RCD; Isermann et al., 2002) was used to index recruitment variability of Bluehead Suckers and Flannelmouth Suckers among rivers. The residual technique uses residuals from catch-curve-like regressions to index recruitment; whereby, positive residuals represent strong year classes and weak year classes are represented by negative residuals (Maceina, 1997). The RCD is the coefficient of determination (r^2) estimated from a catch-curve-like regression (Isermann et al., 2002). Recruitment indices for a given species and river were estimated from years with the highest catch of the species

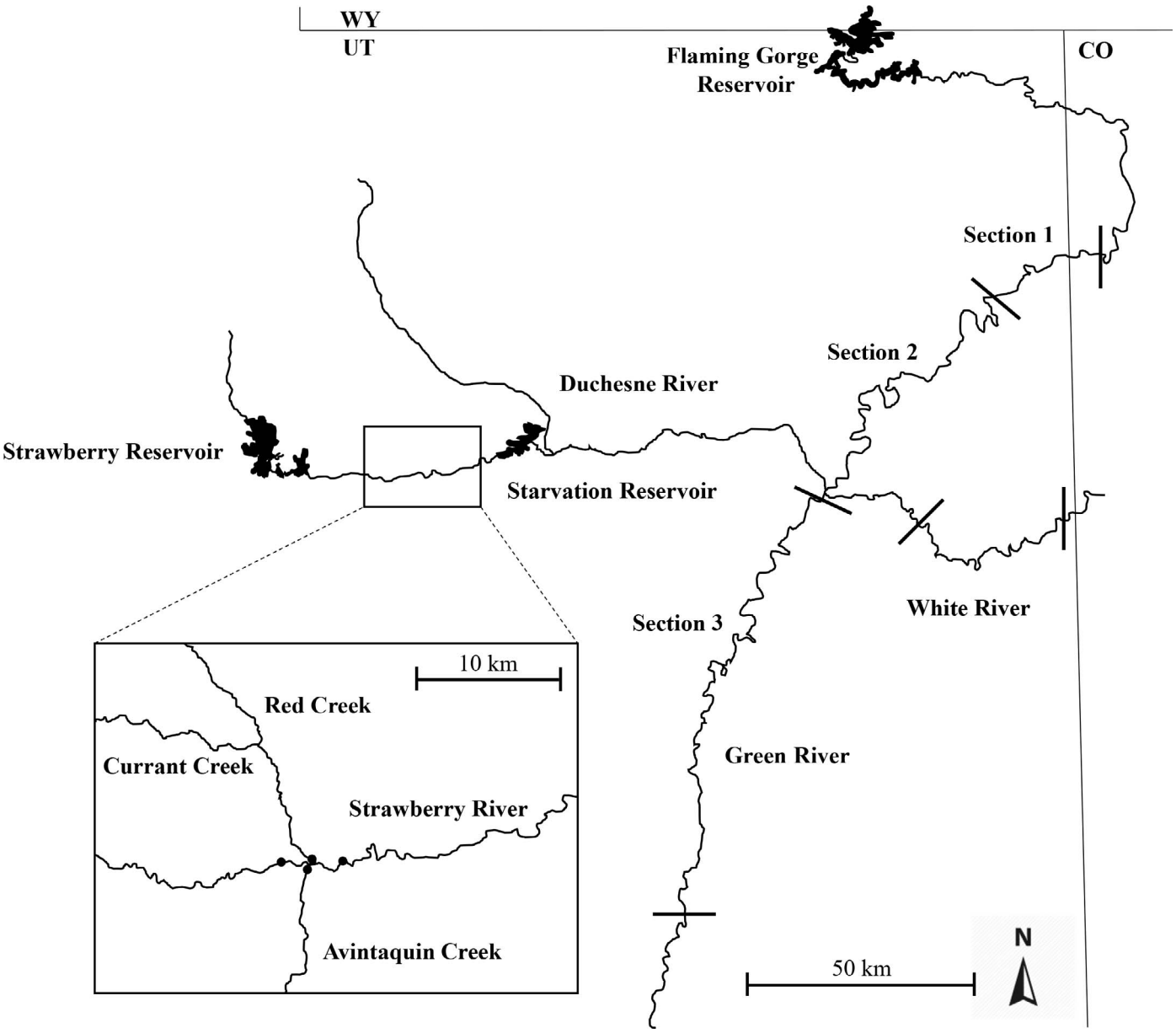

Fig. 1. Sampling sections and reaches for the upper Green, lower Green, Strawberry, and White rivers, Utah. Solid bars represent the beginning and end of sampling sections in the Green and White rivers. Solid circles represent sampling reaches in the Strawberry River.

of interest. Mean back-calculated lengths at age were estimated using the Dahl-Lea method (Quist et al., 2012):

$$L_i = L_c \times (S_i/S_c),$$

where L_i is the length at annulus i, L_c is the length at capture, S_i is the fin ray radius at annulus i, and S_c is the radius at capture. Growth was further summarized by fitting a non-linear function to length-at-age data of Bluehead Suckers and Flannelmouth Suckers (von Bertalanffy, 1938):

$$L_t = L_\infty \left[1 - e^{-K(t-t_0)}\right],$$

where L_t is length at time t, L_∞ is the average maximum length of fish in the population, K is the growth coefficient, t is age, and t_0 is the theoretical age when length equals 0 mm (Isely and Grabowski, 2007; Quist et al., 2012). Models were fit using the fisheries stock assessment (FSA; Ogle, 2010) package in R statistical software (R Development Core Team, 2014).

Understanding the dynamic rate functions of Bluehead Suckers and Flannelmouth Suckers was an important objective of this study. However, we also wanted to examine the potential influence of discharge on the recruitment and growth of Bluehead Suckers and Flannelmouth Suckers. Traditionally, long-term data sets were required to evaluate factors related to variations in growth among years. However, calcified structures (e.g., fin rays) contain data from a fish's entire life and can provide insight on fish growth over multiple years (Weisberg et al., 2010). Somatic growth of fishes is influenced by effects due to age (i.e., size) and the environmental conditions of a given year. Additionally, growth is often correlated within fish and between fish in the same year. As such, a repeated-measures mixed effects model was used to evaluate the factors (age and year) influencing growth of Bluehead Suckers and Flannelmouth Suckers (e.g., Weisberg et al., 2010; Quist and Spiegel, 2012). Repeated measures were taken from individual fish; age was treated as a fixed effect and year was treated as a random

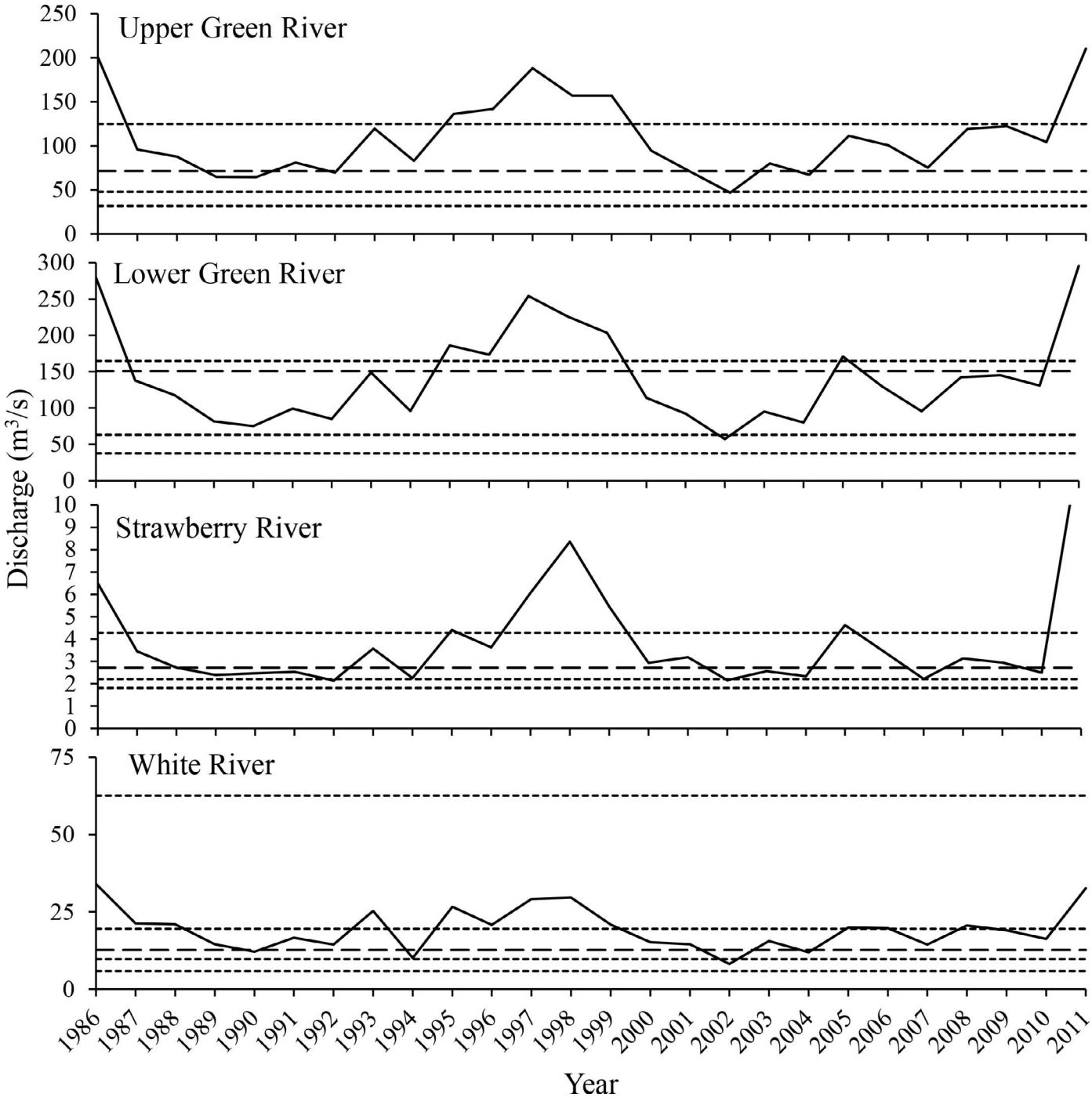

Fig. 2. Mean annual discharge for the upper Green, lower Green, Strawberry, and White rivers, Utah. The dashed line denotes median annual discharge and dotted lines represent 5th, 25th, 75th, and 95th percentiles of annual discharge.

effect. An autoregressive covariance structure was used and models were fit using the R statistical software (R Development Core Team, 2014). Coefficient estimates of growth by year were then used to model the potential influence of discharge on growth for a given species and river.

Discharge (m^3/s) data were obtained from U.S. Geological Survey gaging stations nearest to a study reach (Green River [station numbers = 9315000, 9261000]; Strawberry River [9288180]; White River [9306500]). The period of record varied for each gaging station, but was between 47 and 116 years. Six hydrological indices were used to describe either the magnitude, frequency, or stability of discharge in a given system. The magnitude of flow was summarized as mean annual discharge (Clausen and Biggs, 1997). Drought frequency was estimated as the number of days flows were below the 5th percentile in discharge. Similarly, low-flow events were represented as the number of days discharge was below the 25th percentile (Richter et al., 1998). Flooding and extreme flooding were specified as the number of days flow was above the 75th (flooding) and 95th (extreme flooding) percentile in discharge. Flow stability was characterized as the coefficient of variation (CV) in the number of changes (positive or negative) in water conditions from one day to the next (Wood et al., 2000). All hydrological indices were independent variables in regression models.

An information-theoretic approach was used to select among competing models explaining variability in growth and recruitment (Burnham and Anderson, 2002). Seven candidate models for each species and river section were developed to examine the influence of discharge on growth and recruitment and incorporated one of each hydrological index as a single independent variable. Models were developed using catch-curve residuals (representing year-class strength) and growth increments (coefficient estimates from the repeated-measures mixed effects model) as dependent variables. Akaike's information criterion adjusted for small sample size (AIC_c) was used to compare candidate models and select the best model (i.e., lowest AIC_c value; Burnham and Anderson, 2002). Although AIC_c selects the model with the lowest AIC_c score, competing models could all be poor models. Therefore, model fit was also evaluated using the coefficient of determination (r^2).

RESULTS

In total, 456 Bluehead Suckers and 596 Flannelmouth Suckers were sampled across all rivers (Figs. 3, 4). Age structure varied by species and river. The Green and White rivers had similar age structure for both Bluehead Suckers and Flannelmouth Suckers. For example, Bluehead Suckers in the upper Green River varied in age from 2 to 11 years, whereas Bluehead Suckers in the White River varied in age from 2 to 10 years. Maximum age of Flannelmouth Suckers was 20 years in the upper Green River and 17 years in the White River. Bluehead Suckers and Flannelmouth Suckers exhibited the greatest longevity in the Strawberry River. Flannelmouth Suckers reached a maximum age of 23 years and Bluehead Suckers had a maximum age of 12 years in the Strawberry River. Interestingly, fewer young Flannelmouth Suckers were sampled in the Strawberry River when compared to the Green and White rivers. The mode for Flannelmouth Suckers was age 3 in the lower Green River, whereas the majority of Flannelmouth Suckers in the Strawberry River were between ages 6 and 11.

Estimates of total annual mortality varied from 19% to 44% among species and rivers (Figs. 3, 4). Bluehead Suckers had higher estimates of total annual mortality when compared to Flannelmouth Suckers. For instance, Bluehead Suckers in the Upper Green River had an $A = 40\%$, whereas Flannelmouth Suckers in the same system had an $A = 19\%$. Among rivers, the Strawberry River had the lowest estimated mortality for both species. Similar to total annual mortality, recruitment varied among species and rivers. Bluehead Suckers had fairly stable recruitment across rivers with RCD estimates varying from 0.54 to 0.90 (Fig. 3). Recruitment of Flannelmouth Suckers was less consistent with RCD estimates varying from 0.45 in the lower Green River to 0.77 in the Strawberry River (Fig. 4).

Discharge explained little variation in year-class strength of Bluehead Suckers and Flannelmouth Suckers among rivers (Table 1). Furthermore, the relationship between discharge indices and year-class strength were inconsistent for both species. Top models for Bluehead Suckers included discharge frequency (25^{th} percentile of discharge, 75^{th} percentile of discharge), discharge magnitude (mean annual discharge), and null models. Models relating discharge indices and year-class strength of Flannelmouth Suckers were similarly variable and included 5^{th} percentile of discharge, mean annual discharge, and null models. The direction of influence between discharge indices and year-class strength were variable among rivers for both species (Table 1).

Growth of Bluehead Suckers and Flannelmouth Suckers was fairly consistent among rivers (Fig. 5). For instance, L_∞ only differed among rivers by 50 mm for Flannelmouth Suckers and 34 mm for Bluehead Suckers. The lower Green River had the lowest L_∞ of all rivers for Bluehead Suckers (407 mm) and Flannelmouth Suckers (528 mm). Conversely, the White River had the highest estimate of L_∞ for Bluehead Suckers (499 mm) and Flannelmouth Suckers (578 mm) for all rivers. Similar to year-class strength, variability in growth was poorly explained by discharge covariates (Table 2). However, top models explaining variability in growth were fairly consistent among species and rivers. For example, mean annual discharge was nearly always selected as the top model for Bluehead Sucker. Models explaining variability in growth of Flannelmouth Suckers were less consistent but always included a covariate explaining flow frequency (e.g., 25^{th} percentile of discharge). No clear pattern in the direction of influence between independent variables and growth was apparent among rivers and species (Table 2).

DISCUSSION

Although many native fishes have received considerable attention in the CRB, Bluehead Suckers and Flannelmouth Suckers are among the least-studied species in the system (Bezzerides and Bestgen, 2002). Despite considerable declines in abundance and distribution of Bluehead Suckers and Flannelmouth Suckers in the CRB (Budy et al., 2015), even the most basic information on life-history characteristics is lacking. Nevertheless, a few published studies allow for integration of our results into the existing knowledge of Bluehead Sucker and Flannelmouth Sucker population characteristics. Total annual mortality rates of Bluehead Suckers and Flannelmouth Suckers collected in our study were similar to other populations in the CRB. Bluehead Suckers collected from the Green, Strawberry, and White rivers had an estimated annual mortality rate between 27% and 44%. Walters et al. (2012) reported a similar mortality rate (52%) for Bluehead Suckers collected in the Colorado and Little Colorado rivers, Arizona. Annual mortality rates for Bluehead Suckers collected in tributaries of the Wyoming portion of the Green River (Big Sandy River, Little Sandy Creek, Muddy Creek) varied from 34% to 54% (Sweet et al., 2009). Flannelmouth Suckers generally exhibit lower annual mortality than Bluehead Suckers. In the Colorado and Little Colorado rivers, Arizona, Flannelmouth Suckers had an estimated annual mortality rate of about 20% (Douglas and Marsh, 1998). Similarly, annual mortality rates of Flannelmouth Suckers sampled from Big Sandy River, Little Sandy Creek, and Muddy Creek, Wyoming, were between 14% and 64% (Sweet et al., 2009). In the current study, Flannelmouth Suckers had annual mortality rates between 19% and 36%. Mortality rates of Bluehead Suckers and Flannelmouth Suckers appear to be relatively low, leading some authors to suggest that certain catostomids native to the CRB have been able to adapt to altered flow and temperature regimes characteristic of the system (Mueller and Wydoski, 2004). However, population sustainability is not solely reliant on adult survival, but instead is the result of the dynamics associated with growth, recruitment, and mortality.

Recruitment is often considered to be the primary rate function governing fish populations (Gulland, 1982). As such, understanding the factors that influence year-class

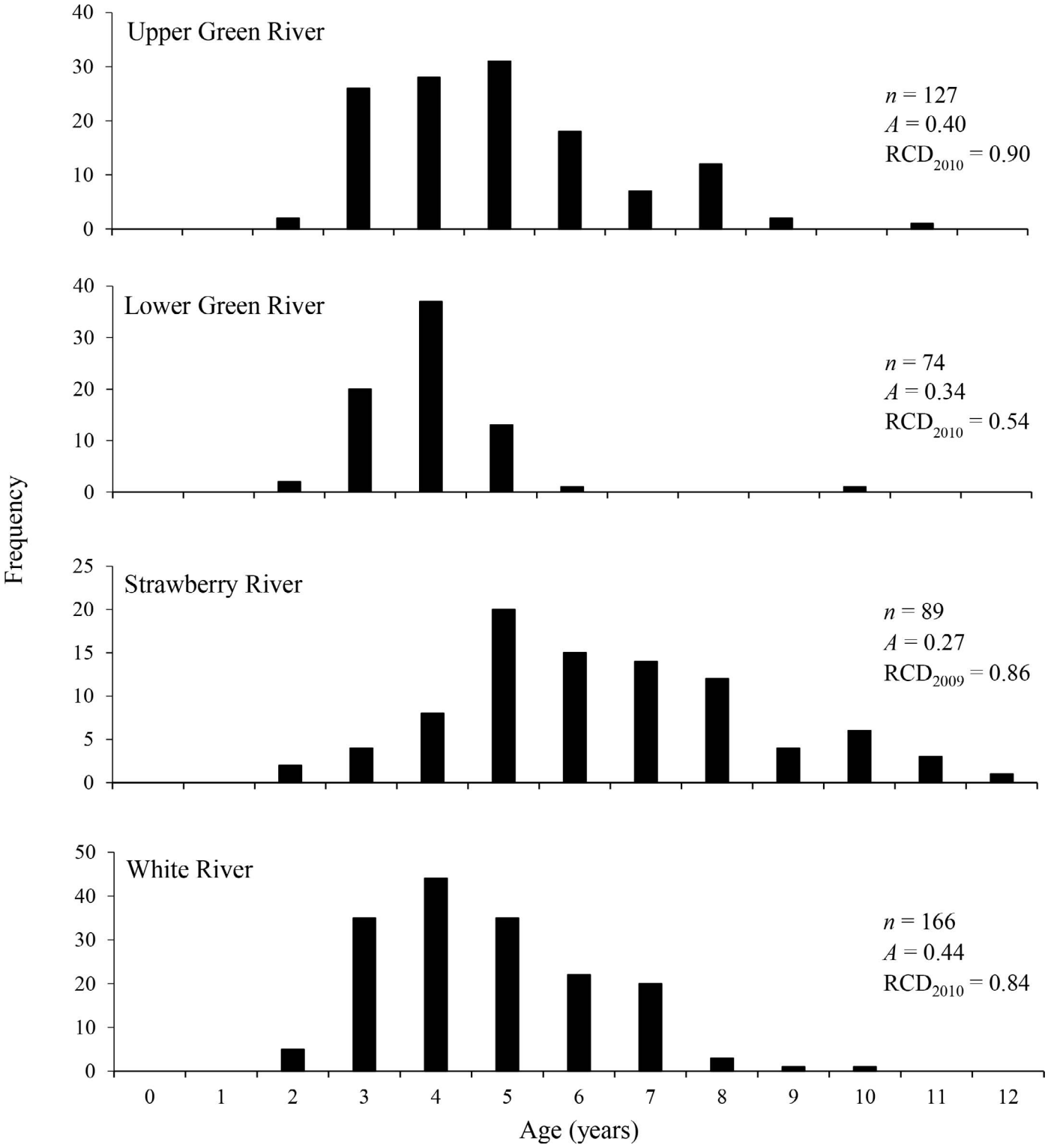

Fig. 3. Age-frequency distributions of Bluehead Suckers sampled from the upper Green, lower Green, Strawberry, and White rivers, Utah. Sample size, annual mortality (*A*), and recruitment coefficient of determination (RCD) are shown for each population. Subscript on RCDs denote the year of capture used to estimate RCD values.

strength and recruitment variability are paramount to effectively managing and conserving fish populations. Our results suggest that Bluehead Suckers and Flannelmouth Suckers in the Green, Strawberry, and White rivers have more stable recruitment when compared to other populations in the CRB. For instance, Flannelmouth Suckers sampled from the Big Sandy River, Little Sandy Creek, and Muddy Creek had RCD values varying from 0.17 to 0.50 (Sweet et al., 2009), whereas RCD values of Flannelmouth Suckers in the Green, Strawberry, and White rivers varied between 0.45 and 0.77. Recruitment indices are not available for other populations, but long-term data suggest that a number of Bluehead Sucker and Flannelmouth Sucker populations exhibit highly variable recruitment. Mueller and Wydoski (2004) sampled Flannelmouth Suckers in the lower Colorado River using trammel nets, hoop nets, minnow traps, and

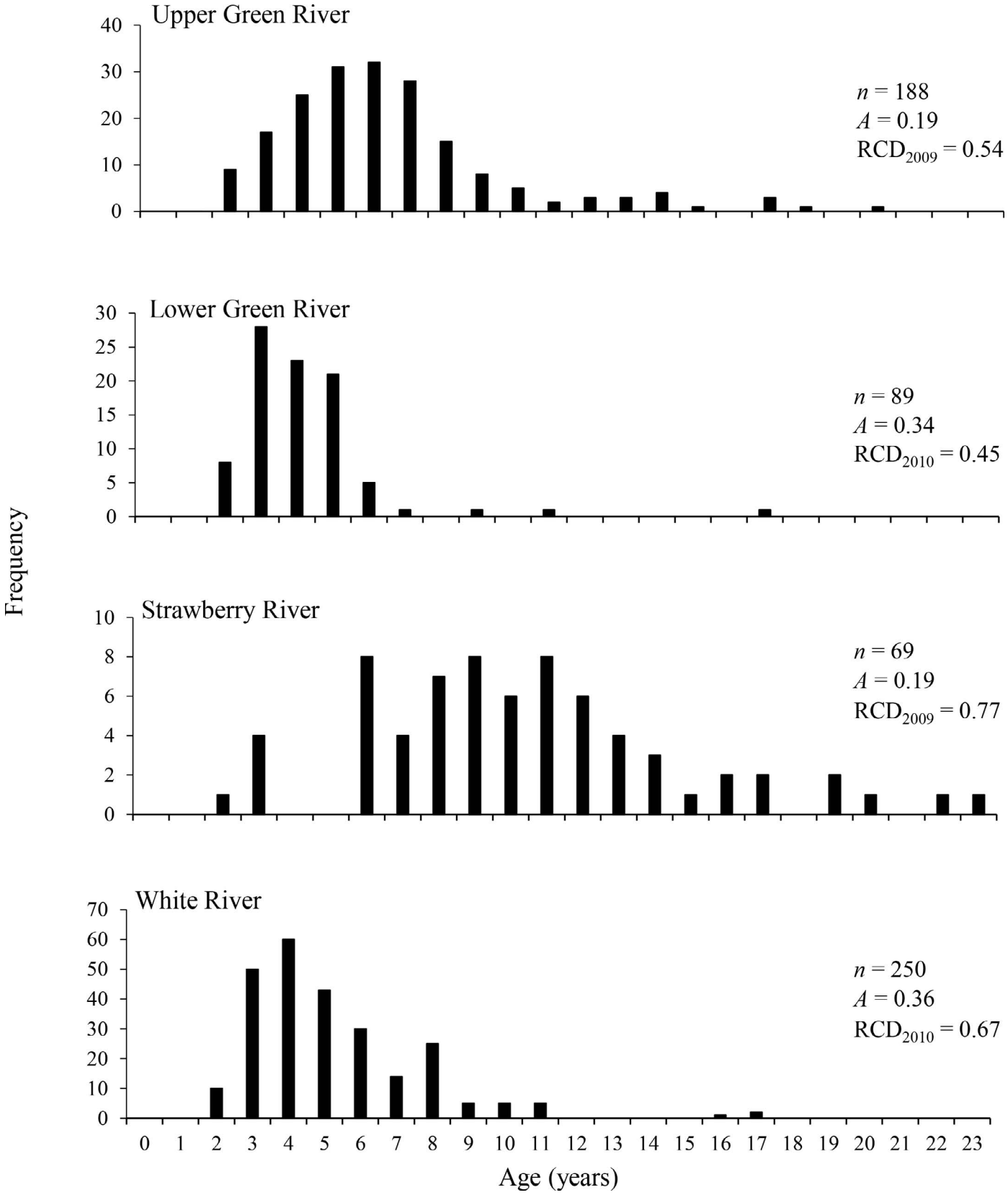

Fig. 4. Age-frequency distributions of Flannelmouth Suckers sampled from the upper Green, lower Green, Strawberry, and White rivers, Utah. Sample size, annual mortality (*A*), and recruitment coefficient of determination (RCD) are shown for each population. Subscript on RCDs denote the year of capture used to estimate RCD values.

light traps. The authors reported that only 5% of the Flannelmouth Suckers sampled were less than 350 mm. Similarly, Weiss (1993) specifically targeted larval Flannelmouth Suckers in the Paria River, Utah, using larval seines (3–5 mm mesh), but failed to sample a single larval fish in 1992 and 1993. The author noted that there was no indication that juvenile Flannelmouth Suckers had reared in the Paria River (Glen Canyon area) in the last 12 years as evidenced by the

Table 1. Regression models predicting year-class strength of Bluehead Suckers and Flannelmouth Suckers sampled from the Green, Strawberry, and White rivers, Utah. Independent variables include the number of days discharge fell below the 5th and 25th percentiles, the number of days discharge exceeded the 75th and 95th percentiles, mean annual discharge, and the coefficient of variation of the number of reversals in discharge. Akaike's information criterion corrected for small sample size (AIC_c), the change in Akaike's information criterion (ΔAIC_c), and Akaike's weight (w_i) were used to evaluate candidate models. Model fit was assessed with the coefficient of determination (r^2). Bold variables indicate a negative relationship.

Species	Model	*K*	AIC_c	ΔAIC_c	w_i	r^2
Green River						
Bluehead Sucker	Null	2	49.74	0.00	0.46	—
	Q_{25}	3	51.76	2.03	0.17	0.16
	Q_{Mean}	3	53.14	3.40	0.08	0.05
	Q_5	3	53.38	3.64	0.07	0.03
	Q_{75}	3	53.44	3.70	0.07	0.02
	Q_{95}	3	53.44	3.70	0.07	0.02
	$Reversals_{cv}$	3	53.66	3.93	0.06	<0.01
Flannelmouth Sucker	Q_5	3	51.33	0.00	0.80	0.37
	Null	2	55.70	4.36	0.09	—
	$Reversals_{cv}$	3	58.26	3.93	0.03	0.03
	Q_{75}	3	58.37	7.04	0.02	0.03
	Q_{25}	3	58.53	7.20	0.02	0.01
	Q_{Mean}	3	58.73	7.40	0.02	<0.01
	Q_{95}	3	58.77	7.44	0.02	<0.01
Strawberry River						
Bluehead Sucker	**Q_{75}**	3	28.43	0.00	0.23	0.07
	Q_5	3	28.81	0.38	0.19	0.02
	Q_{25}	3	28.81	0.38	0.19	0.02
	$Reversals_{cv}$	3	28.88	0.45	0.18	0.01
	Q_{Mean}	3	28.92	0.49	0.18	<0.01
	Null	2	32.65	4.22	0.03	—
Flannelmouth Sucker	Q_{Mean}	3	25.92	0.00	0.73	0.35
	$Reversals_{cv}$	3	30.02	4.11	0.09	0.13
	Q_{25}	3	30.52	4.61	0.07	0.09
	Q_5	3	30.95	5.03	0.06	0.02
	Q_{75}	3	31.61	5.70	0.04	0.01
	Null	2	55.69	29.78	0.00	—
White River						
Bluehead Sucker	Null	2	30.90	0.00	1.00	—
	Q_{Mean}	3	48.90	18.00	0.00	0.08
	$Reversals_{cv}$	3	50.73	19.82	0.00	0.03
	Q_{95}	3	50.77	19.87	0.00	0.03
	Q_{25}	3	50.84	19.94	0.00	0.01
	Q_5	3	50.88	19.98	0.00	<0.01
Flannelmouth Sucker	Null	2	33.81	0.00	0.56	—
	$Reversals_{cv}$	3	37.31	3.50	0.10	0.13
	Q_5	3	37.46	3.65	0.09	0.12
	Q_{Mean}	3	37.49	3.68	0.09	0.12
	Q_{95}	3	38.23	4.42	0.06	0.04
	Q_{75}	3	38.47	4.66	0.05	0.01
	Q_{25}	3	38.56	4.75	0.05	<0.01

scarcity of larval Flannelmouth Suckers in the system since 1981. Considering the life-history characteristics of Bluehead Suckers and Flannelmouth Suckers, inconsistent recruitment reported in much of the CRB is not surprising. Many of the "big-river" fishes (e.g., Bluehead Suckers, Flannelmouth Suckers) native to the CRB have adapted to the harsh, unpredictable environment by increased fecundity and longevity (Bezzerides and Bestgen, 2002; Mueller and Wydoski, 2004). The high reproductive output and long life span characteristic of fishes native to the CRB allows for low recruitment and/or periodic recruitment failure (Stearns, 1977). However, alterations to the natural flow and temperature regimes likely exacerbate natural variations in recruitment.

Recruitment is influenced by myriad factors; however, streamflow is generally considered an important characteristic governing recruitment of many fishes endemic to the CRB (Muth et al., 2000; Valdez and Nelson, 2004; Webber et al., 2012; Webber and Haines, 2014; Bestgen and Hill, 2016). During high-flow events, fishes have access to floodplain habitats to obtain resources and reproduce. Additionally, backwater habitats created by high-flow events serve as important nursery habitats for juvenile fishes (Junk et al., 1989; Poff et al., 1997; Muth et al., 2000; Poff and Zimmerman, 2010). As such, high-flow events and the resulting increase in backwater habitats have been shown to be important determinants to recruitment success of juvenile fishes. Bower et al. (2008) reported a positive relationship between occurrence of juvenile Bluehead Suckers and

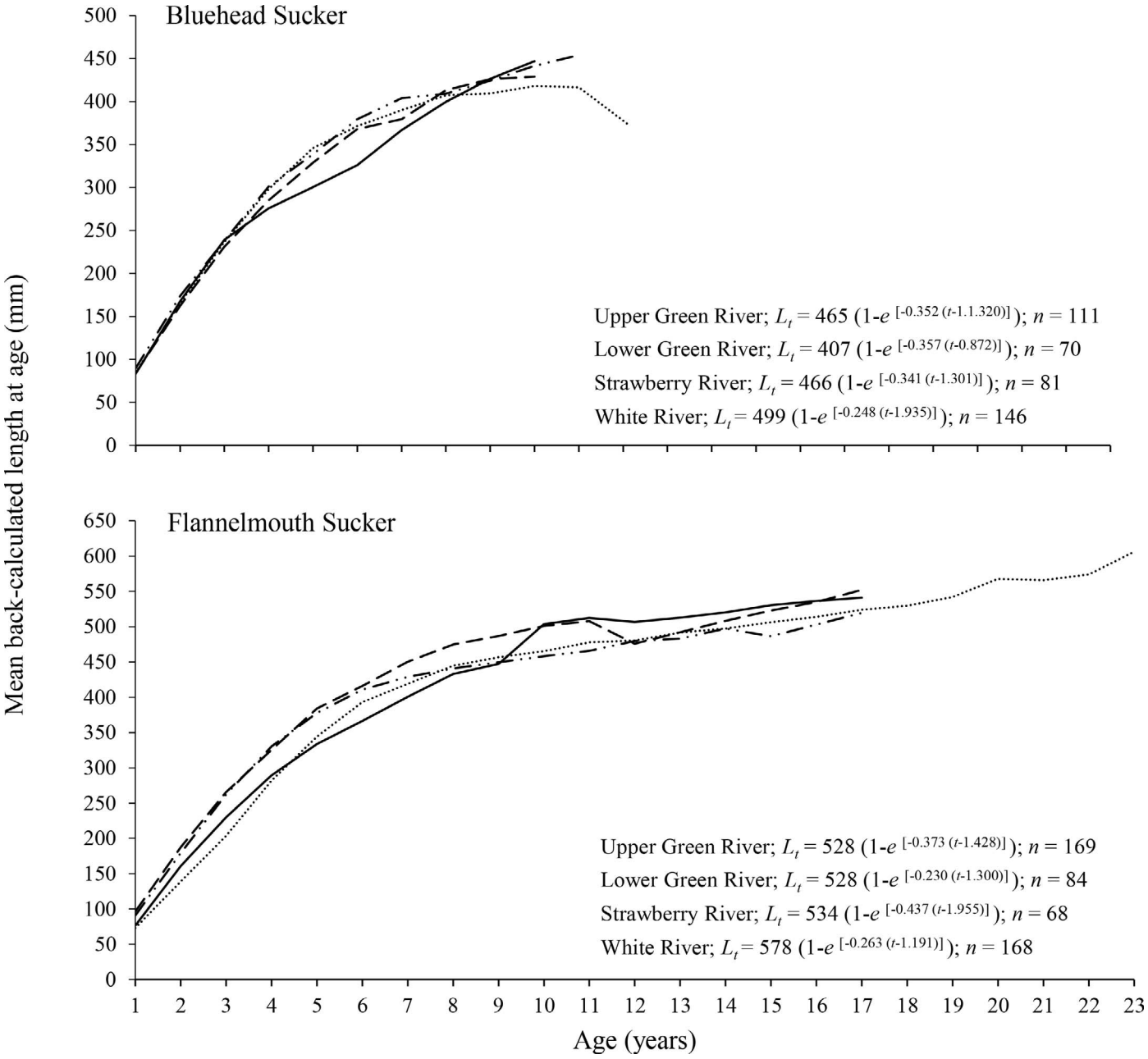

Fig. 5. Mean back-calculated length at age for Bluehead Suckers and Flannelmouth Suckers sampled from the upper Green (dash-dot line), lower Green (solid line), Strawberry (dotted line), and White (dashed line) rivers, Utah. Von Bertalanffy models and sample sizes are included for each population.

Flannelmouth Suckers and surface area of pool habitat in Muddy Creek, Wyoming. The timing of reproduction and larval abundance of Colorado Pikeminnow was positively related to the magnitude of peak spring runoff in the Green and Yampa rivers (Bestgen and Hill, 2016). Quist and Guy (1998) reported an increase in Channel Catfish (*Ictalurus punctatus*) recruitment during high-flow years in the Kansas River, Kansas. Despite the importance of discharge to recruitment of juvenile fishes, none of our models relating year-class strength and discharge had any explanatory power. Similarly, Quist and Spiegel (2012) reported a weak relationship between the 75th percentile in discharge and recruitment of eight catostomids in four Iowa rivers. Although models relating year-class strength and discharge had poor fit, our results are likely indicative of a lag between hydrological events and their resulting effect on recruitment and mortality. In long-lived species (e.g., Bluehead Suckers, Flannelmouth Suckers), mortality occurs over a long time period during which time fish can experience high variability in biotic and abiotic factors (Mauck and Boxrucker, 2004; Kwak et al., 2006). Despite poor model fit, the relatively stable recruitment exhibited by Bluehead Suckers and Flannelmouth Suckers in the current study suggest that the Green, Strawberry, and White rivers have adequate rearing habitats to support periodic recruitment success.

Similar to recruitment, growth is particularly important with regard to the ecology and population characteristics of fishes (Quist et al., 2012). Nearly every event in a fish's life is influenced by size. Thus, growth directly influences survival and reproduction and can provide insight on factors influencing fish populations (e.g., resource availability). Growth of native suckers in the Green, Strawberry, and

Table 2. Regression models predicting growth of Bluehead Suckers and Flannelmouth Suckers sampled from the Green, Strawberry, and White rivers, Utah. Independent variables include the number of days discharge fell below the 5th and 25th percentiles, the number of days discharge exceeded the 75th and 95th percentiles, mean annual discharge, and the coefficient of variation of the number of reversals in discharge. Akaike's information criterion corrected for small sample size (AIC_c), the change in Akaike's information criterion (ΔAIC_c), and Akaike's weight (w_i) were used to evaluate candidate models. Model fit was assessed with the coefficient of determination (r^2). Bold variables indicate a negative relationship.

Species	Model	*K*	AIC_c	ΔAIC_c	w_i	r^2
Green River						
Bluehead Sucker	**Q_{Mean}**	3	67.80	0.00	0.45	0.23
	$Reversals_{cv}$	3	68.85	1.04	0.27	0.18
	Null	2	70.73	2.92	0.11	—
	Q_{25}	3	72.19	4.38	0.05	0.05
	Q_{75}	3	72.38	4.57	0.05	0.05
	Q_5	3	72.52	4.71	0.04	0.04
	Q_{95}	3	73.17	5.37	0.03	0.01
Flannelmouth Sucker	**Q_{25}**	3	54.02	0.00	0.24	0.07
	Null	2	54.03	0.01	0.24	—
	Q_5	3	55.19	1.17	0.13	0.04
	$Reversals_{cv}$	3	55.33	1.31	0.12	0.03
	Q_{Mean}	3	55.67	1.65	0.10	0.02
	Q_{95}	3	55.94	1.92	0.09	0.02
	Q_{75}	3	56.45	2.43	0.07	<0.01
Strawberry River						
Bluehead Sucker	Q_{Mean}	3	18.02	0.00	0.32	0.27
	Null	2	18.68	0.66	0.23	—
	Q_5	3	19.07	1.06	0.19	0.21
	Q_{25}	3	20.91	2.89	0.08	0.09
	$Reversals_{cv}$	3	21.02	3.00	0.07	0.08
	Q_{95}	3	21.22	3.21	0.07	0.07
	Q_{75}	3	22.15	4.13	0.04	<0.01
Flannelmouth Sucker	**Q_5**	3	26.27	0.00	0.35	0.14
	Null	2	27.23	0.97	0.22	—
	$Reversals_{cv}$	3	28.28	2.01	0.13	0.06
	Q_{75}	3	28.73	2.46	0.10	0.05
	Q_{25}	3	29.64	3.37	0.07	<0.01
	Q_{95}	3	29.65	3.38	0.07	<0.01
	Q_{Mean}	3	29.69	3.43	0.06	<0.01
White River						
Bluehead Sucker	Null	2	13.23	0.00	0.55	—
	Q_{Mean}	3	15.91	2.69	0.14	0.15
	Q_{25}	3	16.79	3.56	0.09	0.07
	$Reversals_{cv}$	3	17.04	3.81	0.08	0.05
	Q_5	3	17.25	4.02	0.07	0.03
	Q_{95}	3	17.47	4.25	0.07	<0.01
Flannelmouth Sucker	Q_{75}	3	23.61	0.00	0.60	0.28
	Null	2	26.69	3.08	0.13	—
	Q_{Mean}	3	27.09	3.48	0.11	0.13
	Q_5	3	28.37	4.76	0.06	0.07
	$Reversals_{cv}$	3	28.53	4.92	0.05	0.06
	Q_{25}	3	29.60	5.99	0.03	<0.01
	Q_{95}	3	29.60	5.99	0.03	<0.01

White rivers was higher compared to other populations in the CRB. For instance, Flannelmouth Suckers in Little Sandy Creek, Wyoming, averaged 36 mm of growth a year from age 0 to 7 (Sweet et al., 2009), whereas Flannelmouth Sucker in the White River averaged 50 mm of growth over the same time period. Bluehead Suckers in the current study exhibited similarly high growth when compared to other populations. For example, age-10 Bluehead Suckers in the Green River were on average 67 mm longer than age-10 fish sampled from the Big Sandy River, Wyoming, and 128 mm longer than age-10 fish sampled in Muddy Creek, Wyoming (Sweet et al., 2009). High growth rates of Bluehead Suckers and Flannelmouth Suckers in the Green, Strawberry, and White rivers are likely indicative of favorable environments conditions (e.g., water temperature, prey availability). However, identifying environmental factors contributing to high growth rates of Bluehead Suckers and Flannelmouth Suckers in the Green, Strawberry, and White rivers remains difficult.

Variability in discharge and resulting nutrient inputs are often hypothesized to be the predominant factor contributing to the productivity of lotic systems (Junk et al., 1989; Thorpe and Delong, 1994; Tockner et al., 2000). Natural river fluctuations (e.g., contractions and expansion of the main channel) enhance riparian-river interactions and ultimately the input of terrestrially derived nutrients (Tockner et al., 2000). Although access to the floodplain is limited by the

morphology of a system (e.g., canyons, levees), even localized flooding and high flows can result in a net increase in nutrients in the main channel (Vannote et al., 1980; Junk et al., 1989). Consequently, the relationship between fish growth and discharge has received considerable attention. Growth of Channel Catfish was positively related to flooding in the Kansas River (Quist and Guy, 1998). The frequency of flooding (number of days discharge exceeded the 75th percentile) in four Iowa rivers explained 50–70% of the variation in growth of eight catostomid species (Quist and Spiegel, 2012). In the central Amazon River, growth of omnivorous fishes was 60% faster during flood conditions (Bayley, 1988). Considering the results of other studies, poor model fit relating growth and discharge characteristics in our study was surprising. However, certain features of water development in much of the CRB may help explain our results. Water development such as levees and channelization reduce overbank flow (Daniels, 1960; Prestegaard et al., 1994) and disconnect the main channel from its floodplain. Therefore, fishes may not benefit from flooding events as might be expected (Rutherford et al., 1995). The Colorado River and its tributaries have undergone extensive water development over the last century resulting in significant changes to channel morphology (Van Steeter and Pitlick, 1998). For example, the main-stem Colorado River lost approximately 25% of side channel and backwater habitats and has narrowed by an average of 20 m from 1937 to 1993. Similar changes in the Green, Strawberry, and White rivers would likely result in a reduction in main channel-floodplain interaction and the apparent discontinuity between growth and flooding events. Although discharge likely affects growth of fishes in the CRB, other environmental characteristics may have a more significant influence on fish growth.

Changes to the thermal regime are often implicated as contributing to the decline of native fishes in the CRB (Muth et al., 2000; Bezzerides and Bestgen, 2002). Water temperatures directly influence somatic growth (Gorman and VanHoosen, 2000; Robinson and Childs, 2001) and indirectly influence survival and recruitment (Kaeding and Osmundson, 1988; Valdez and Ryel, 1995; Haines et al., 1998; Bestgen and Crist, 2000). Unfortunately, long-term water-temperature data were not available in the Green, Strawberry, and White rivers, limiting our ability to evaluate the influence of water temperature on growth. Notwithstanding, results of other studies suggest that water temperature is an important mediating factor in regard to fish growth. Growth of age-0 Humpback Chub, Speckled Dace (*Rhinichthys osculus*), Flannelmouth Sucker, and Bluehead Sucker were positively correlated with water temperature in the Little Colorado River (Robinson and Childs, 2001). The authors suggested that age-0 fish migrating to the Colorado River would exhibit significant retardation in growth and would be subject to increased predation, size-dependent competition, and other cold-related stressors (e.g., cold coma) due to unfavorable water temperatures. Gorman and VanHoosen (2000) experimentally evaluated the influence of water temperature characteristic of the Colorado and Little Colorado rivers (12°C, 18°C, 24°C) on the growth of Humpback Chub, Bonytail, Bluehead Sucker, and Razorback Sucker. The authors reported that all species exhibited greatest growth at 24°C and concluded that temperatures typical of cold tailwaters (12°C) would increase mortality of fishes inhabiting the mainstem Colorado River downriver of Glen Canyon Dam. Given the ubiquity of dams and resulting cold-water hypolimnetic releases in the CRB, alterations to the thermal regime will likely pose a challenge to the conservation of native fishes.

Human-induced changes to lotic systems pose a risk to native fishes worldwide (Poff et al., 1997; Cooke et al., 2005). In the CRB, alterations to flow and temperature regimes are often posited as negatively influencing native fish populations. Despite the likely negative effects of water development on native fishes, our results indicate that Bluehead Suckers and Flannelmouth Suckers in the Green, Strawberry, and White rivers represent fairly stable populations. However, slow growth, poor recruitment, and high mortality rates exhibited in other populations suggest that the populations in the current study are the exception rather than the rule. Although substantial work has been conducted to mediate the negative influences of water development in the CRB (e.g., Muth et al., 2000; Bezzerides and Bestgen, 2002), few studies have been able to identify the mechanism(s) leading to population declines. Population declines signify a disequilibrium among dynamic rate functions. A basic understanding of the demographics and dynamics of fish populations represents the first step in effectively managing and conserving fishes endemic to the CRB. Once population demographics and dynamics are understood, scientists can begin to disentangle the complex interaction between fishes and altered flow regimes in the CRB and rivers worldwide.

ACKNOWLEDGMENTS

We thank P. Abate, S. Ackerman, D. Allen, M. Ault, P. Badame, N. Berndt, K. Bjerke, C. Black, N. Boren, J. Bransky, K. Breidinger, R. Brunson, B. Carlswell, B. Clyde, L. Cooper, R. Fedelleck, E. Freeman, C. Griffith, A. Hansen, T. Hedrick, J. Hojohn, K. Holt, L. Horzepa, J. Huber, L. Imlay, J. Jimenez, E. Johnson, J. Johnson, L. Johnson, S. Jones, T. Jones, S. Keddy, B. Keifer, D. Keller, D. Lepeparo, Z. Lowe, K. McAbee, C. Mangen, L. Marthe, W. Massure, B. McDonald, S. McKay, M. McKell, C. Mellon, K. Mullen, J. Murray, R. Mosely, T. Perank, A. Rasmussen, K. Sadlier, R. Schmaltz, R. Schneidervin, M. Smith, K. Uhler, A. Vande Voort, M. Warder, B. Wessman, S. Wilkens, and R. Wirick who assisted with field work. M. Fiorelli assisted with data management and organization. We thank B. Compton for helpful comments on a previous version of this manuscript. Funding for the project was largely provided by the Endangered Species Mitigation Fund, Utah State Wildlife Grants, and the Bureau of Land Management Fisheries Program. Additional support was provided by the U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit. The Unit is jointly sponsored by the U.S. Geological Survey, University of Idaho, and Idaho Department of Fish and Game, and Wildlife Management Institute. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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