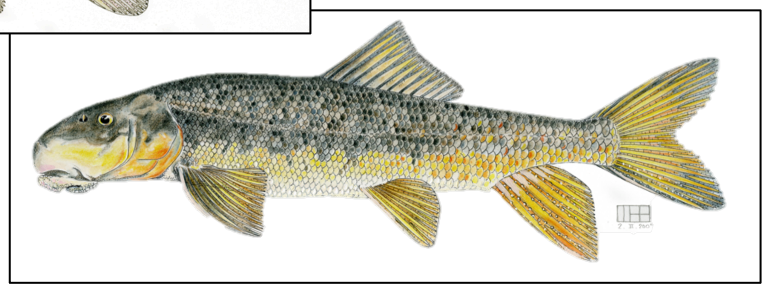
REPRODUCTIVE ECOLOGY AND EARLY LIFE HISTORY OF BLUEHEAD SUCKER AND FLANNELMOUTH SUCKER IN THE SAN JUAN RIVER



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FINAL REPORT

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New Mexico Department of Game and Fish
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EXECUTIVE SUMMARY

Bluehead and Flannelmouth Suckers are native to the San Juan River where flow is largely regulated by input from the Animas River and releases from Navajo Reservoir. Dams may result in hypolimnial release of cold water and modifications to natural flow regimes, thus altering the conditions to which native fishes had evolved. Water temperature, a primary cue for spawning of Bluehead and Flannelmouth Suckers, also mediates growth rate, incubation time, and hatch dates. This study seeks to document reproductive ecology and early life history of Bluehead and Flannelmouth Suckers by determining growth rates and spawn dates, investigating the relationship between fish length and daily age, and examining the impacts of Growing Degree–Days (GDD) on growth rates and spawn dates.

Larval fishes were collected from nursery habitat in the San Juan River once a week from 22 April 2011 to 29 July 2011, preserved in 95% EtOH and transported to the Museum of Southwestern Biology, University of New Mexico where they were identified to species, ontogenetic stage was determined, and body length (Standard Length; SL) was measured. A subset of Bluehead and Flannelmouth Sucker larvae from each weekly sample was designated for otolith removal and sagittal and lapillus otoliths removed from the left side of the head, mounted on a glass microscope slide, and aged by two independent readers. Otolith age was used to calculate daily growth rates, hatch dates, and spawn dates and to develop a growth curve to describe the relationship between age and body length. Three growth curves, von Bertalanffy, Gompertz, and logistic, were evaluated with Akaike's Information Criterion for best fit. Growing degree–days were used to determine the impact of thermal time on growth rates and spawn dates.

Bluehead Suckers ranged from 9.5–21.3 mm SL and ages ranged from 7–50 days while Flannelmouth Suckers ranged from 12.5–26.7 mm SL and ages ranged from 10–60 days. The relationship between length and age (in days) was best described by a logistic growth model for both Bluehead and Flannelmouth Suckers. Growth rates of Flannelmouth Suckers ranged from 0.12–0.47 mm/day and were poorly correlated with GDD (r = -0.42, $P < 0.001$). Likewise, growth rates of Bluehead Suckers ranged from 0.00–0.37 mm/day and were poorly correlated with GDD (r = -0.21, $P < 0.001$). For both species, larvae produced earlier in the season, those with more accumulated GDD since hatching, had lower growth rates than recently produced larvae. Growing degree–days are likely a better metric for describing growth rate of larval fishes when used on a single cohort instead of all larvae produced in a season.

Flannelmouth Suckers spawned earlier than Bluehead Suckers in the San Juan River. Spawning dates of Flannelmouth Sucker ranged from 17 March 2011 to 20 June 2011, while spawning dates of Bluehead Sucker ranged from 12 April 2011 to 6 July 2011. Spawning dates of Bluehead Suckers (R^2 = 0.95, $P < 0.001$) and Flannelmouth Suckers (R^2= 0.95 $P < 0.001$) were positively related to GDD. Although Bluehead and Flannelmouth Suckers had different thermal preferences and spawned at different times of the year, both spawned when few or zero GDD had been accumulated. Flannelmouth Suckers in the San Juan River spawned at similar temperatures to other drainages while the minimum temperature at which Bluehead Suckers spawn in the San Juan River may be lower than previously recorded in other rivers.

INTRODUCTION

Bluehead Sucker *Catostomus discobolus* and Flannelmouth Sucker *Catostomus latipinnis* are catostomids native to the San Juan River and the Colorado River Basin (Sublette et al. 1990; Carman 2007). Both Bluehead and Flannelmouth Suckers were historically widespread within the basin, but are now restricted to 45% and 50% of their former ranges respectively (Bezzerides and Bestgen 2002). Introduction of nonnative predators and effects of dams are thought to have contributed to range reduction of these two species (Carman 2007).

Human demand for water has resulted in construction of more than a dozen major dams in the Colorado River Basin (Clarkson and Childs 2000). Dams may result in hypolimnial release of cold water, alterations to the natural flow regimes, and barriers to movement, among other effects, thus altering the conditions under which native fishes had evolved (Clarkson and Childs 2000; UDWR 2006; Webber et al. 2012). Flannelmouth Suckers have been documented making seasonal migrations to spawning habitat, and dams may obstruct these migrations or interfere with environmental cues for spawning among native fishes. Among abiotic conditions, water temperate is a primary cue for spawning of Flannelmouth and Bluehead Suckers (Bezzerides and Bestgen 2002), and cool water temperatures may delay spawning (Webber et al. 2012). Low temperature may also decrease hatching success of sucker eggs (Bozek et al. 1990) and increase incubation time (Haines 1995; Zelasko et al. 2011).

Bluehead and Flannelmouth Suckers co-occur throughout the Colorado River Basin; however, they use different habitats. In the San Juan River, Bluehead Suckers are commonly found in faster moving water than Flannelmouth Suckers and prefer habitat with fast flowing water over rocky substrate (Holden 1999; Carman 2007). Flannelmouth Suckers utilize pools, runs, eddies, and riffles with a variety of substrates including gravel, rock, sand or mud (Holden 1999; Bezzerides and Bestgen 2002; UDWR 2006; Carman 2007). In the San Juan River, Bluehead and Flannelmouth Suckers spawn in spring and early summer (Bezzerides and Bestgen 2002; Farrington et al. 2015). Eggs of both Bluehead and Flannelmouth Suckers are demersal and initially adhesive (Holden 1999). Sucker larvae are associated with low velocity habitats such as backwaters, eddies, and shorelines (Holden 1999; Carman 2007).

Spawning periodicity can be difficult to document by direct observation; however, spawning periodicity may be back calculated by counting daily growth increments—consisting of alternating opaque and translucent bands—deposited on otoliths of larval fishes. Use of otolith microstructure analysis to back-calculate spawn and hatch dates is a technique that is commonly used in fisheries and has been used extensively within the Colorado River Basin. In most fish species, increments are deposited from hatch at a rate of one per day (Campana and Neilson 1985, Bundy and Bestgen 2001), and these increments may be counted to obtain age in days.

Bundy and Bestgen (2001) determined that larvae of Razorback Sucker *Xyrauchen texanus*, a federally endangered catostomid of the Colorado River Basin, deposit otolith increments daily from hatch under both fluctuating and stable temperature conditions. Using this information, hatch and spawn dates may be back calculated to document the timing of spawning and hatching and elucidate the abiotic conditions that were present during these events. In the upper Colorado River Basin, a study on the invasive Smallmouth Bass *Micropterus dolomieu* determined that they deposit otolith increments at a rate of one per day (Hill and Bestgen 2013). This information allows for accurate back-calculation of hatch date, which may be used to control Smallmouth Bass populations. Specifically, in the dam-regulated Green River, resource managers may be able to use hatch date information to create a disturbance in order to interrupt spawning and prevent recruitment to the population (Hill and Bestgen 2013). Conversely, in systems such as the San Juan River, knowledge of hatch and spawn dates may be used to enhance spawning by native species rather than disrupting it. Aging otoliths from every larvae captured can be costly and time consuming. Fish length is often used as a surrogate for age, but without species-specific equations derived for individual rivers, such information may be misleading. Development of age–length curves for Bluehead and Flannelmouth Suckers in the San Juan River will allow future hatch and spawn dates to be estimated from body length.

Otolith microstructure analysis can also be used to determine somatic growth rates of larval fishes. Length and rapid growth of larval fishes are positively correlated with survival due to an improved ability to feed and avoid predators (Rice et al. 1993; Campana 1996). Larval suckers may become less susceptible to predation at around 25 mm Total Length (TL), so rapid growth may increase survival (Bestgen 2008). Many factors, including temperature, influence growth rate of larval fish; in the Colorado

River Basin, temperature has a positive correlation with growth rate of larval fish (Clarkson and Childs 2000; Bestgen 2008). Determination of the influence of temperature on somatic growth rate of larval Bluehead and Flannelmouth Suckers in the San Juan River may guide decisions about maintenance and creation of nursery habitat.

The San Juan River Basin Recovery Implementation Program (SJRBRIP) was created in 1991 to recover populations of endangered Colorado Pikeminnows *Ptychocheilus lucius* and Razorback Suckers within the San Juan River while allowing water development to proceed (San Juan River Basin Recovery Implementation Program 2012). The actions of the program to recover and protect endangered species also benefit native species, including Bluehead and Flannelmouth Suckers. Long term monitoring, including sub-adult and adult large bodied fish community monitoring, is conducted annually, and a valuable long-term dataset for Bluehead and Flannelmouth Suckers has been created. During monitoring activities, Flannelmouth Suckers are typically the most abundant large-bodied fish species collected while Bluehead Suckers are typically the second most abundant (Schleicher 2014). Over the past 15 years, there has been no significant change in abundance of adult and sub-adult Bluehead or Flannelmouth Suckers (Schleicher 2014). Populations of both Bluehead and Flannelmouth Suckers have varied over time, but overall have remained stable (Carman 2007).

In 2003, New Mexico, Arizona, Colorado, Utah, Wyoming, and Nevada entered into a range-wide conservation agreement for Roundtail Chub *Gila robusta*, Bluehead Suckers, and Flannelmouth Suckers with the goal of ensuring persistence of these species in their current ranges. Among the conservation actions listed in the conservation agreement is "Determine Roundtail Chub, Bluehead Sucker, and Flannelmouth Sucker population demographics, life history, habitat requirements, and conservation needs." Basic abundance, distribution, and life history of Bluehead and Flannelmouth Suckers are known within the San Juan River due to SJRBRIP studies, but no study has been undertaken specifically to document reproductive ecology or early life history of Bluehead and Flannelmouth Suckers.

Objectives

Management Issue 3 in the New Mexico Sucker Conservation Strategy states "aspects of population demographics, life history, habitat requirements, and conservation needs of Bluehead and Flannelmouth Suckers are poorly understood in the Colorado River basin (Carman 2007)." This study provides life history information (spawning periodicity) of these species via the following objectives.

1. Determine daily growth rates of Bluehead and Flannelmouth Sucker larvae.
2. Investigate relationship between fish length and daily age.
3. Investigate relationship between growth rates of fishes and growing degree-days (GDD).
4. Determine spawning dates for adult Bluehead and Flannelmouth Suckers.
5. Investigate relationship between spawning dates and GDD.

Study area

The San Juan River originates in the San Juan Mountains in southern Colorado and flows approximately 350 miles before its terminus in Lake Powell. It is a major tributary to the Colorado River and drains approximately 38,000 mi^2 in Colorado, New Mexico, Arizona, and Utah (USFWS 2012). The San Juan River is impounded by Navajo Dam and discharge is largely controlled by releases from Navajo Reservoir (Propst and Gido 2004). In addition to impoundment by Navajo Dam, several diversions reduce flows in the San Juan River including the Fruitland Irrigation Canal, Hammond Canal, Farmers Mutual Ditch, Four Corners Power Plant, San Juan Generating Station, and Hogback Canal (USFWS 2012). Riparian vegetation along the San Juan River consists of Tamarisk *Tamarix spp.*, Russian olive *Elaeagnus angustifolia,* Fremont cottonwood *Populus fremontii,* and willow *Salix spp.*; however, Tamarisk and Russian olive dominate riparian vegetation.

Larval fishes were collected from nursery habitats at three sites in close proximity: the confluence of an unnamed wash with the San Juan River at River Mile (RM) 99.3 (UTM Coordinates: 658634 E, 4121397 N, Zone 12 S, WGS84), the confluence of Allen Canyon with the San Juan River at RM 96.4 (UTM Coordinates: 654507 E, 4123859 N, Zone 12 S, WGS84), and the confluence of Recapture Creek with the San Juan River at RM 84.1 (UTM Coordinates: 635395 E, 4127547 N, Zone 12 S, WGS84; Figure 1). Sites were chosen due to their close proximity to the NM border (within one day drift of larval fish), the presence of low velocity habitat, and abundance of larval suckers.

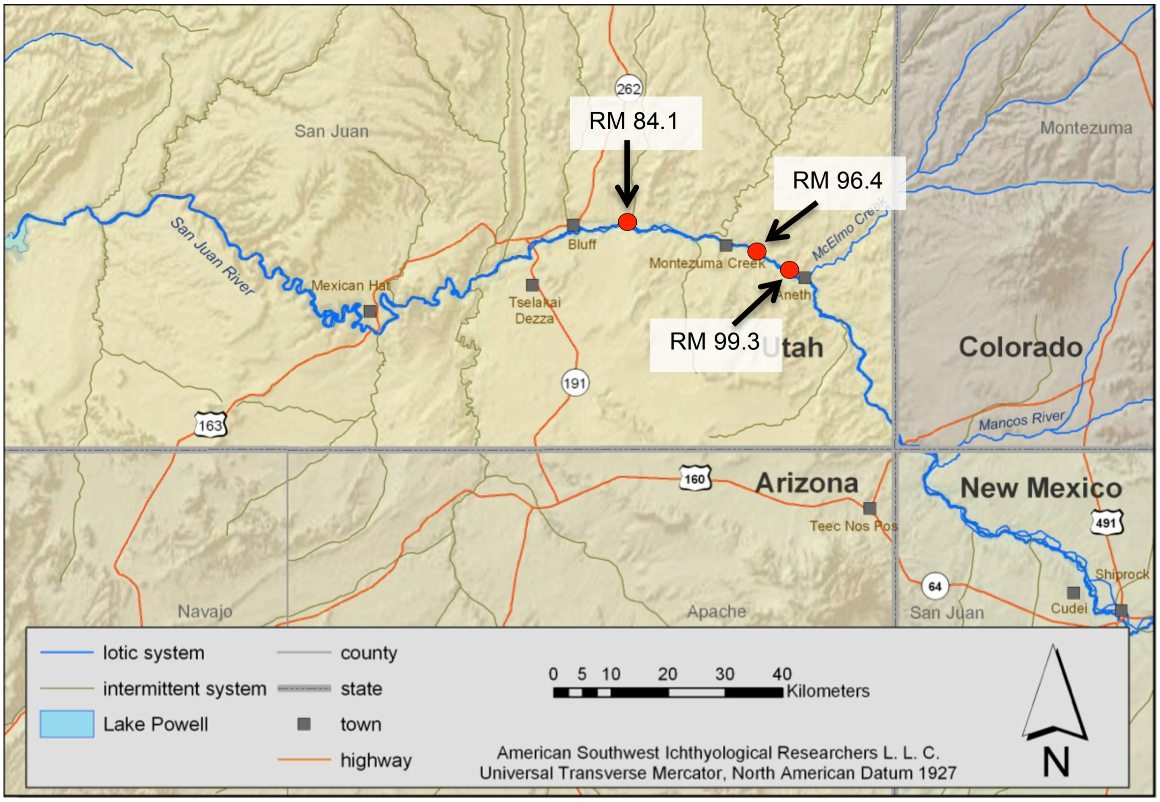

Figure 1. Location of larval fish collection study sites (denoted by red dots) on the San Juan River and associated River Miles (RM).

METHODS

Once a week from 22 April 2011 to 29 July 2011, larval fishes were collected with a fine mesh larval seine (1 m x 1 m x 1.5 mm mesh). Larval fishes cannot be identified in the field, so retained specimens were preserved in 95% EtOH and transported to the Museum of Southwestern Biology, University of New Mexico. Larval fish were identified to species under stereo-microscopes with transmitted light bases and polarized light filters by personnel with expertise in identification of San Juan River larval fishes, enumerated, measured (total [TL] and standard length [SL]), and ontogenetic stage was determined. Weekly samples were combined to provide sufficient material for this study.

Age and growth

A subset of Bluehead Sucker and Flannelmouth Sucker larvae from each weekly sample (n = 1–34) representing the range of lengths present was designated for otolith removal. Otoliths were removed under stereo-microscopes with transmitted light bases and polarized filters. On the left side of the fish's head, a series of small, shallow incisions were made with an insect pin (size 00 or 000) inserted into a micro dissecting needle holder. The small incisions allowed the top layer of tissue to be lifted off and removed. At this point, otoliths could be seen glowing brightly under polarized light and were removed with the tip of the insect pin. Otoliths were difficult to differentiate under a stereo-microscope, so all otoliths, the sagitta, lapillus, and asteriscus, were removed from the left side of the fish. All extracted otoliths from a single fish were mounted on a 25 x 75 mm glass microscope slide between two short pieces of 0.10 mm diameter UTC ultra wire (Wapsi, Mountain Home, AR, USA) to prevent otoliths from being crushed, embedded in Crystalbond 509 (SPI supplies, West Chester, PA, USA), and covered with a glass cover slip.

Mounted otoliths were viewed with a Zeiss Axioskop 2 MAT 50-1,000X compound microscope using oil immersion lenses and viewed using the magnification that most clearly showed growth rings. Lapilli were preferentially used for aging because they were typically larger than sagittae and because at larger sizes, sagittae grew fragile projections that were easily broken. Lapilli are commonly used in age and growth studies involving suckers because they are larger and less delicate than sagittae (Thompson and Beckman 1995; Hoff et al. 1997; Sylvester and Berry 2006). In instances where the lapillus was unusable (i.e. not removed, broken, obscure) the sagitta was used for age determination. Sagittae and lapilli have been shown in other catostomids to accumulate growth rings at the same rate (Bundy and Bestgen 2001; Song et al. 2008). Two independent readers aged otoliths by counting daily increments from the primordium to the edge of the otoliths (Figure 2). Disagreements between readers were reconciled during a joint reading. If disagreements could not be reconciled, the sample was recorded as unreadable and not included in analyses.

Daily growth rates between hatching and date of capture were calculated by subtracting length at hatching from length at capture and dividing by the age of the fish in days as determined by counting daily growth increments on otoliths. Length of Flannelmouth Suckers at hatching was 10–11 mm SL and length of Bluehead Suckers at hatching was 9–10 mm SL (Snyder and Muth 2004); for this study, length at hatching was assumed to be 10.5 mm SL for Flannelmouth Suckers and 9.5 mm SL for Bluehead Suckers.

Numerous growth curves have been utilized to describe growth of larval fishes. The von Bertalanffy Growth Function (VBGF) is the most frequently used growth model in fisheries and is frequently used *a priori* (Katsanevakis 2006; Helidoniotis et al. 2011). However, in many cases, alternate growth functions, such as Gompertz or logistic, are more appropriate for fitting age and length data (Zweifel and Lasker 1976; Katsanevakis and Maravelias 2008). Accurate model selection is important to prevent over or underestimating parameters. Relationship between age and growth was evaluated using the VBGF, Gompertz, and logistic growth functions (Ogle 2015). Model selection was performed using Akaike's information criterion (AICc) (Helidoniotis et al. 2011; Ogle 1015); lower AICc values indicate better fit of the data to the model.

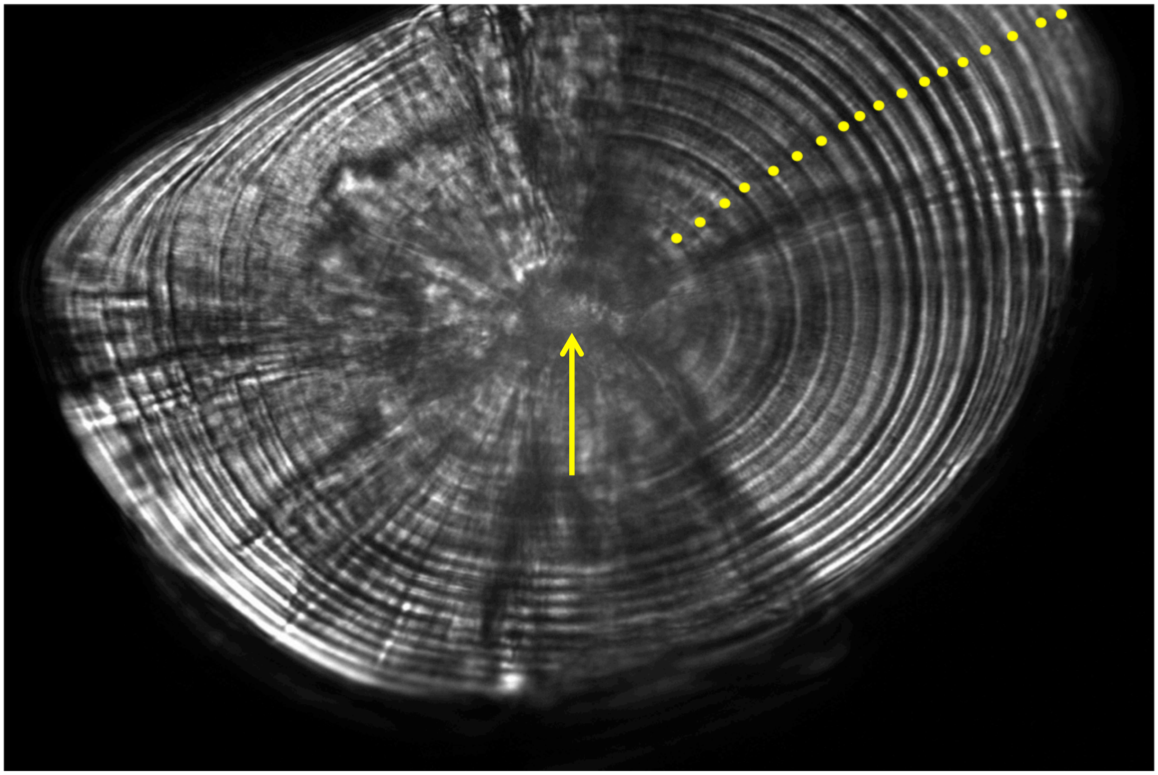

Figure 2. Primordium (yellow arrow) and daily growth increments (marked with yellow dots) of an 18 day old larval Flannelmouth Sucker.

Incubation time

Incubation times of Bluehead and Flannelmouth Suckers were estimated using the equation:

$$y = \frac{(4.125(T_{avg})^2 - 163.5(T_{avg}) + 1764)}{24}$$

which, although extrapolated from incubation times for Flannelmouth Suckers, has been used to calculate incubation time for other sucker species including Bluehead Suckers (Zelasko et al. 2011). In the equation, T_{avg} is the mean water temperature on the day when fish hatched.

Spawning date

Spawning dates were calculated by subtracting the incubation time from the hatch date. Hatch dates were determined by subtracting a fish's age in days, as determined by otolith increment counts, from the collection date.

Degree days

Growing degree-days are a thermal integral concept that measures thermal time, or physiologically relevant temperature (Neuheimer et al. 2008), and are used to measure the cumulative thermal growing time for an organism. Growing degree-days have been used for many years for agricultural uses and are applicable to most fishes because they are ectothermic and their metabolisms are dependent on temperature (Neuheimer and Taggart 2007). Thus, in most cases, GDD may be a reliable predictor of fish growth and development. Daily water temperatures, recorded at the USGS gage near Bluff, UT (#09379500) were obtained for GDD analysis. Initial attempts to record water temperature in sampled habitats failed due to drying of habitats, which left temperature loggers out of water. The USGS San Juan River Bluff, UT gage has recorded water temperature since 2007 and is located <20 RM downstream from the most upstream larval sucker sampling site. This close proximity makes this gage an appropriate source for mainstem water temperatures for this study. Daily water temperatures were used to calculate daily GDD using the equation

$$\text{GDD} = T_{avg} - T_{base}$$

where T_{base} is the minimum water temperature below which the process of interest (spawning), does not exist, and T_{avg} is the mean daily water temperature; because GDD are a measure of physiologically relevant temperature, only temperatures greater than T_{base} are included in the calculation. Cumulative GDD were calculated by summing daily GDD to represent how warm the overall growing season has been. Cumulative GDD were calculated for spawn date and collection date. Collection date was used as an end date for calculation of growth rate. Bluehead Sucker spawn at temperatures of 15–18°C (Snyder and Muth 2004), so 15°C, the minimum extreme of the temperature range, was used for T_{base}. Flannelmouth Suckers likely spawn at cooler temperatures, and female Flannelmouth Suckers become ripe at 10°C (UDWR 2006), so 10°C was used for T_{base} . Growing degree-days may provide valuable information on growth of larval Bluehead and Flannelmouth Suckers and may be used to predict spawning dates. The relationship between GDD and spawning date was evaluated using nonlinear regression. A Pearson product-moment coefficient of correlation and linear regression were used to determine the relationship between GDD and growth rate of larvae.

RESULTS

Bluehead Suckers (n = 263) and Flannelmouth Suckers (n = 255) were examined from collections made in 2011. Bluehead Suckers ranged from 9.5–21.3 mm SL and ages ranged from 7–50 days. Flannelmouth Suckers ranged from 12.5–26.7 mm SL and ages ranged from 10–60 days. Specimens of Bluehead and Flannelmouth Suckers represented a range of larval ontogenetic stages from protolarvae to metalarvae. No other life stages were included in these analyses.

Age and growth

Logistic, Gompertz, and von Bertalanffy growth functions were fitted to both datasets and ranked by AICc weights and AICc values (Table 1). Although all growth models were closely ranked, the logistic growth model was the highest ranked model for describing the relationship between age and length for both Bluehead and Flannelmouth Suckers (Figure 3 and Figure 4). Parameter estimates (where a = asymptote, r = growth rate/day, and b = inflection point) were obtained from the logistic growth model and applied to a logistic growth equation:

$$\text{age (days)} = \left[\frac{ln\left(\frac{a}{L}-1\right)}{-r}\right] + b$$

to describe the relationship between age and growth for each species. The relationship between age and length of Bluehead Sucker larvae is described by the equation:

$$\text{age (days)} = \left[\frac{ln\left(\frac{85.23}{L}-1\right)}{-0.018}\right] + 113.90$$

where *L* is Standard Length (SL) of an individual fish in mm. The relationship between age and length in Flannelmouth Sucker larvae is described by the equation:

$$\text{age (days)} = \left[\frac{ln\left(\frac{30.68}{L}-1\right)}{-0.028}\right] + 17.84$$

A growth equation was only generated for the logistic growth model because it was the highest ranked model for describing relationship between age and length in both Bluehead and Flannelmouth Suckers.

Growth rates of Bluehead Suckers ranged from 0–0.37 mm/day and were poorly correlated with GDD (Pearson product-moment coefficient of correlation: r = -0.21, d.f. = 261, $P < 0.001$). There was a poor relationship between growth rate and GDD for Bluehead Suckers ($R^2 = 0.03$, $P < 0.01$; Figure 5). Likewise, growth rates of Flannelmouth Suckers ranged from 0.12–0.47 mm/day and were poorly correlated with GDD (Pearson product-moment coefficient of correlation: r = -0.42, d.f. = 253, $P < 0.001$). There was a poor relationship between growth rate and GDD for Flannelmouth Suckers ($R^2 = 0.02$, $P < 0.001$; Figure 6).

Spawning dates

Spawning dates of Bluehead Suckers ranged from 12 April 2011 to 6 July 2011 with the majority of spawning dates occurring in May and June while spawning dates of Flannelmouth Sucker ranged from 17 March 2011 to 20 June 2011, with the majority of spawn dates occurring in April and May (Figure 7). Spawning dates of Bluehead and Flannelmouth Suckers are positively related to GDD (Figure 8 and Figure 9). In Bluehead Suckers, 95% of variance in spawn dates can be explained by GDD ($R^2 = 0.95$, $P< 0.001$) while in Flannelmouth Suckers, 99% of variance in spawn dates can be explained by GDD ($R^2 = 0.99$, $P < 0.001$).

Table 1. Logistic, Gompertz, and von Bertalanffy growth functions for Bluehead and Flannelmouth Suckers age and length data. Models are ranked using Akaike's information criterion (AICc).

Models	K	AICc	AICcWT
Bluehead Suckers			
Logistic	4	780.17	0.34
Gompertz	4	780.20	0.33
von Bertalanffy	4	780.22	0.33
Flannelmouth Suckers			
Logistic	4	892.21	0.34
Gompertz	4	892.23	0.34
von Bertalanffy	4	892.28	0.33

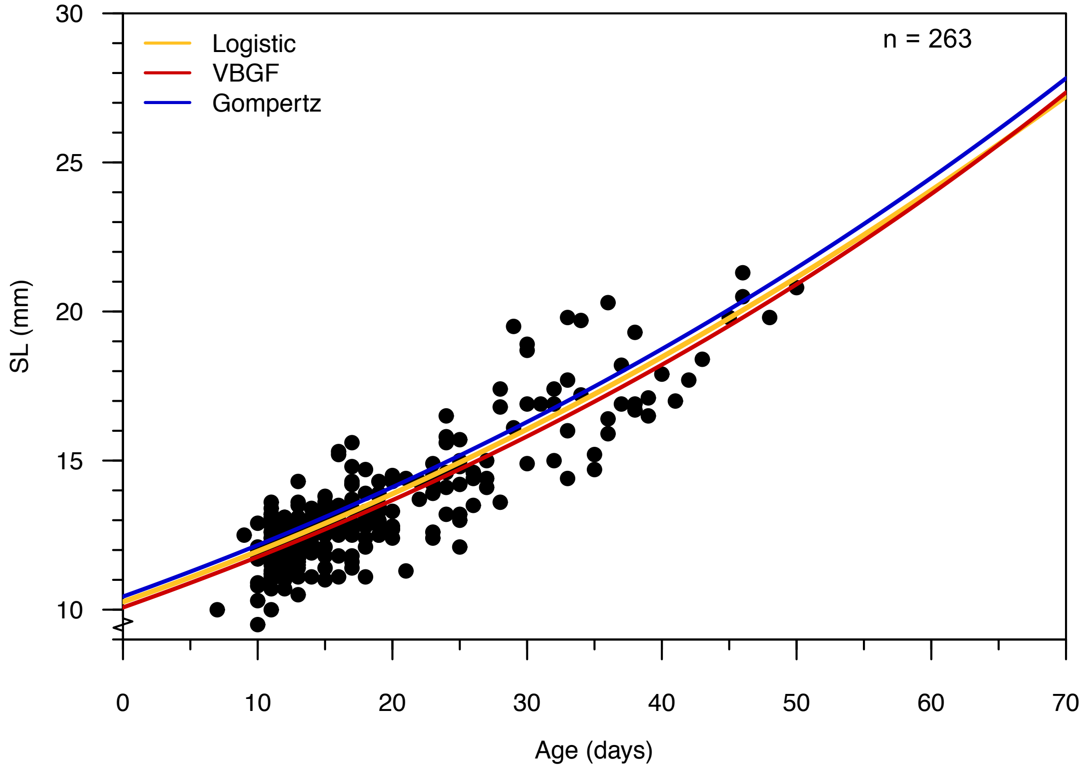

Figure 3. Best-fit models for logistic, von Bertalanffy growth function (VBGF), and Gompertz growth functions for the relationship between age–length of Bluehead Sucker larvae.

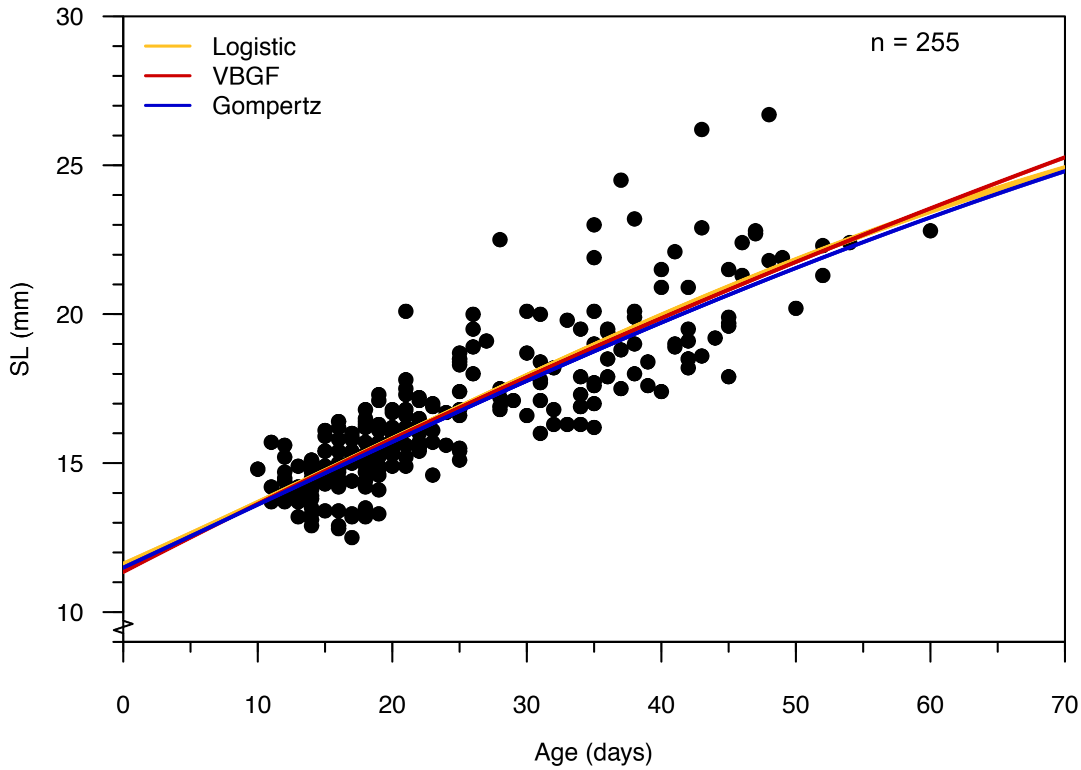

Figure 4. Best-fit models for logistic, von Bertalanffy growth function (VBGF), and Gompertz growth functions for the relationship between age–length of Flannelmouth Sucker larvae.

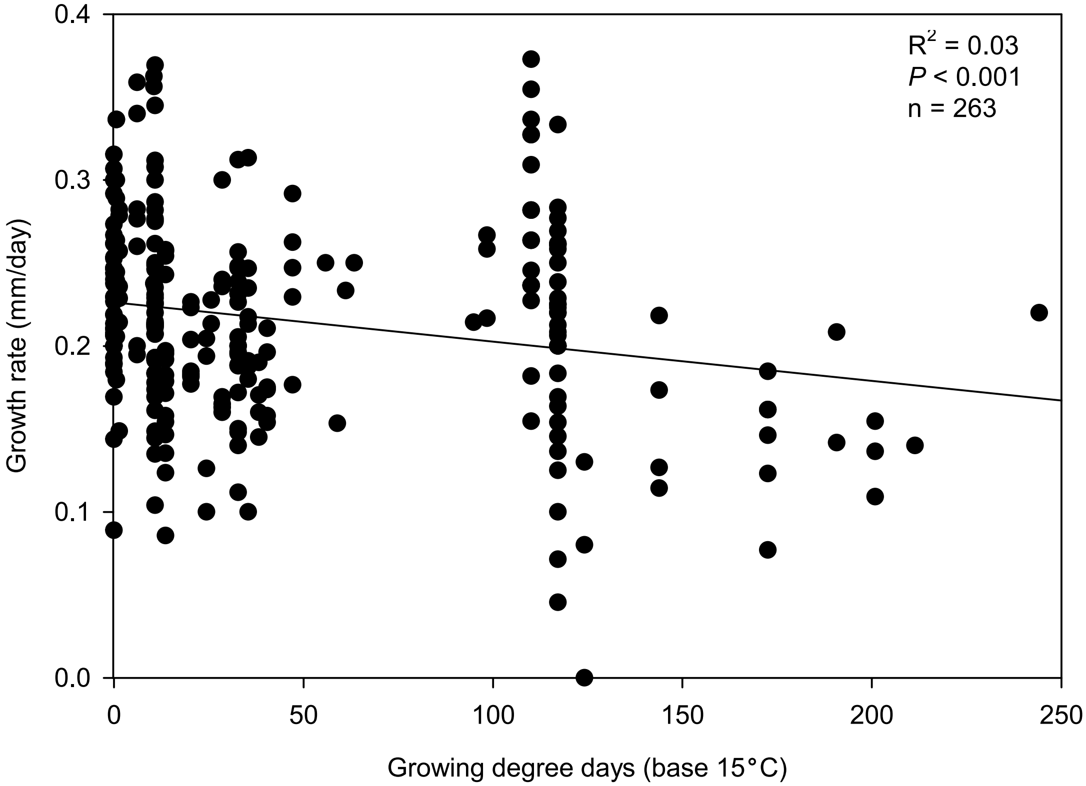

Figure 5. Relationship between growth rate and accumulated growing degree-days (GDD) of Bluehead Sucker larvae.

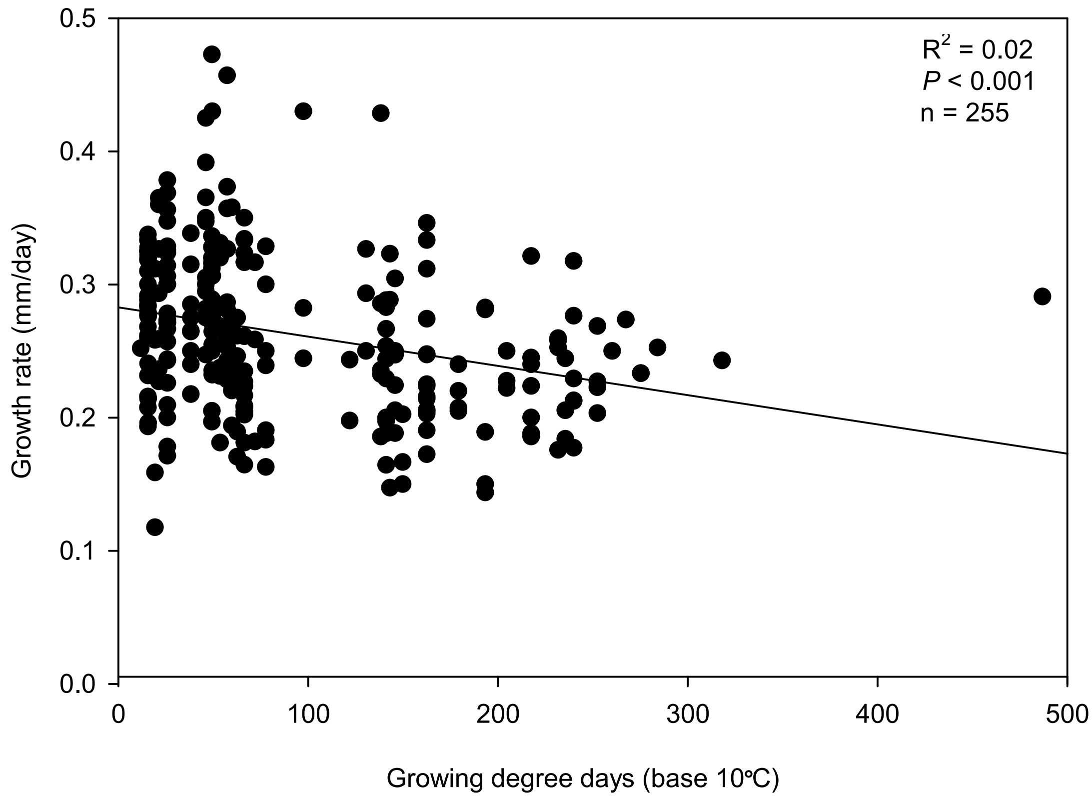

Figure 6. Relationship between growth rate and accumulated growing degree-days (GDD) of Flannelmouth Sucker larvae.

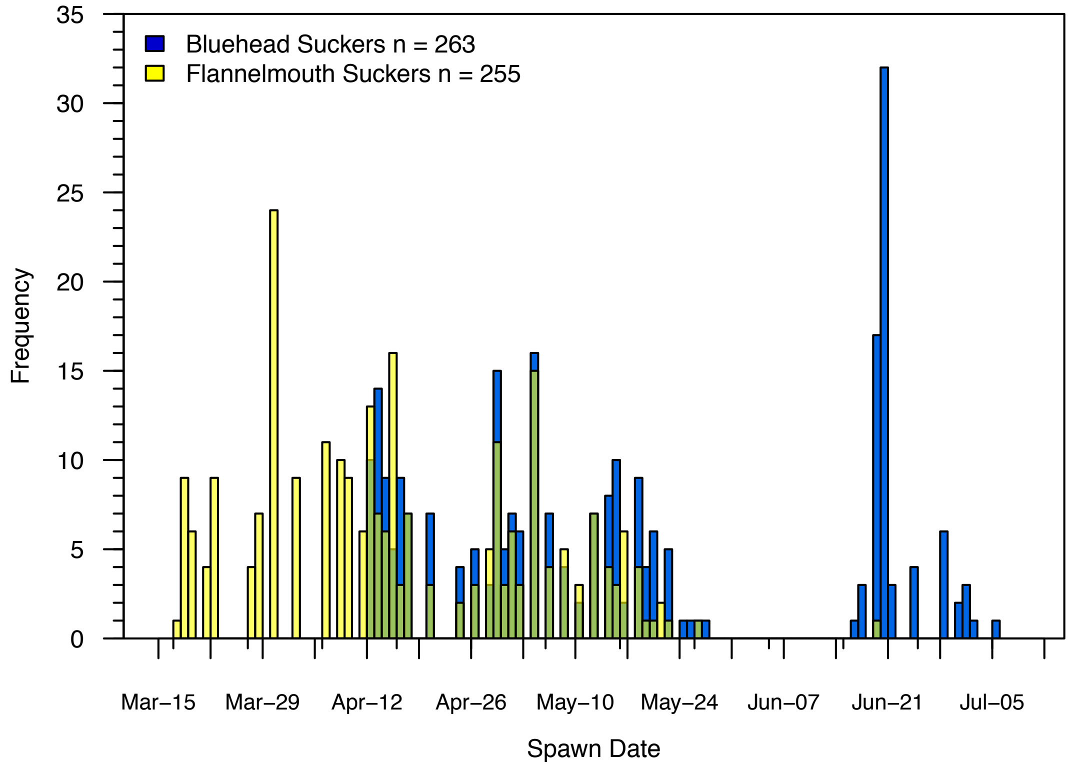

Figure 7. Bluehead Sucker and Flannelmouth Sucker spawn dates in the San Juan River. Overlap of Bluehead Sucker and Flannelmouth Sucker spawning dates creates green bars.

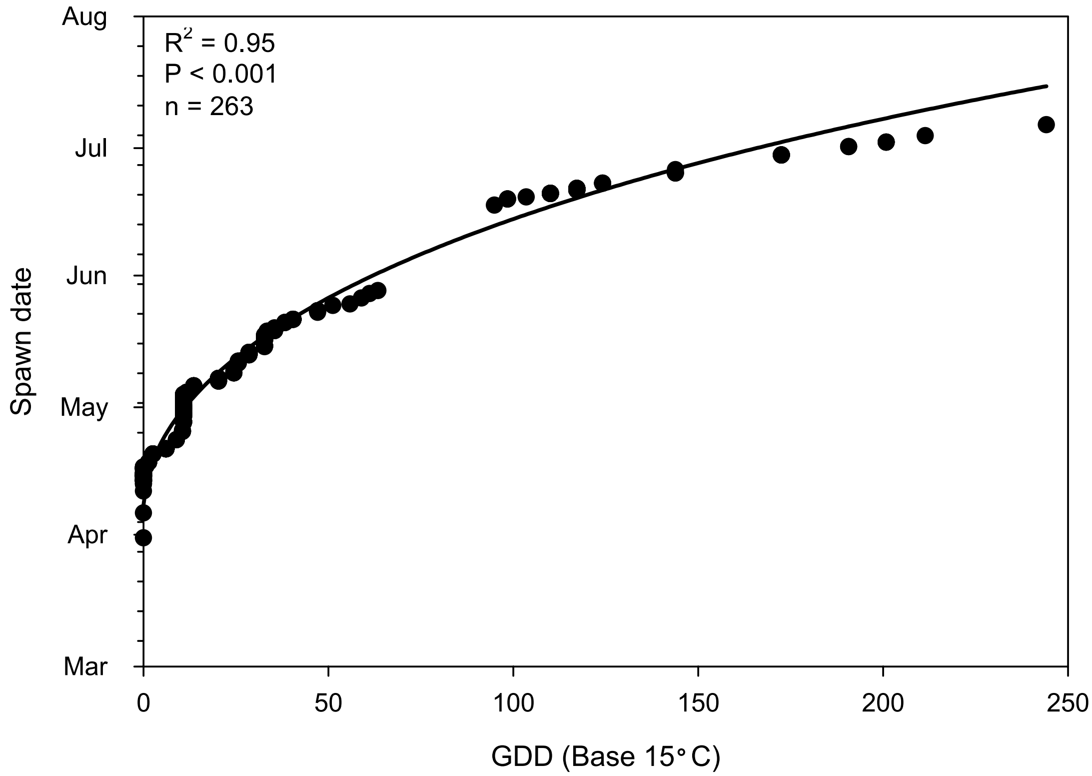

Figure 8. Spawning dates of Bluehead Suckers as a function of growing degree-days (GDD) in the San Juan River.

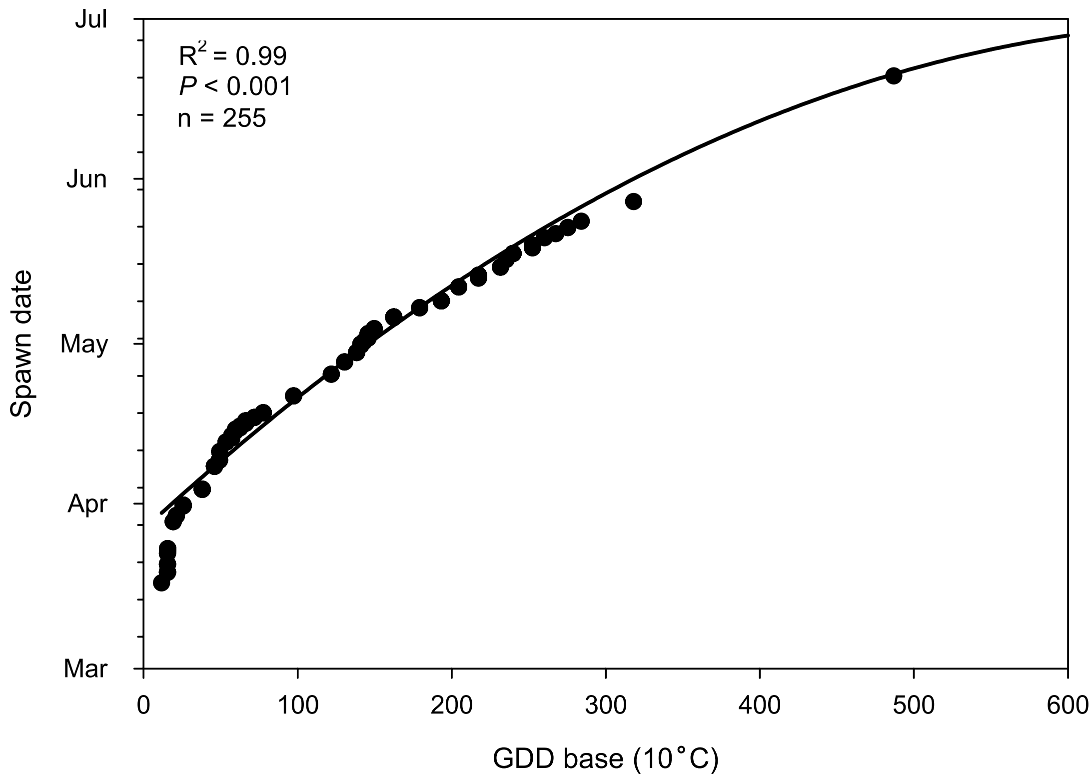

Figure 9. Spawning dates of Flannelmouth Suckers as a function of growing degree-days (GDD) in the San Juan River.

DISCUSSION

The relationship between age and length of larvae was described by a logistic growth curve for both Bluehead and Flannelmouth Suckers, and the logistic growth curve was better suited for the analyses than either Gompertz or von Bertalanffy growth curves. However, due to the similarity of AICc values between the models, it is likely that all would be suitable for predicting age based on fish length. Although, the logistic, von Bertalanffy, and Gompertz growth curves were similar throughout most of the age ranges for both species, the models tended to differ toward older ages, so model choice could skew age–length calculations of larger larvae. The equations produced by the logistical growth curves have great utility for informing management decisions and allow age estimation for larval fishes without the time consuming removal and aging of otoliths. Estimated hatch dates may be calculated by subtracting the estimated age calculated from the equations from the date the larvae were collected. Additionally, spawning periodicity may be estimated by pairing estimated hatch dates with an equation to estimate incubation times (Zelasko et al. 2011). Spawn dates and hatch dates provide information about when larval fishes are produced and present in the river and are important for guiding management decisions regarding when to release water into the river to ensure the presence of nursery habitat.

The relationship between somatic growth of fishes and temperature is well documented (Clarkson and Childs 2000; Uphoff et al. 2013) with increased growth rate at warmer temperatures (Bestgen 2008). Accelerated growth of larval fishes is positively correlated with survival due to an improved ability to feed and avoid predators (Campana 1996). Previous studies have found a positive relationship between accumulated GDD and fish size (Neuheimer and Taggart 2007; Uphoff et al. 2013). In this study, however, there was poor relationship between growth rate and GDD for both Bluehead and Flannelmouth Suckers, which was likely related to the large variation in sizes and growth rates. Both Bluehead and Flannelmouth Suckers had continuous spawning during the study period, producing multiple cohorts of fish and multiple size classes resulting in large variation in growth rate. For both species, larvae that were produced earlier in the season (those with higher GDD) tended to have lower growth rates than recently produced larvae (those with lower GDD). Larvae that were produced earlier in the season were exposed to cooler temperatures, which likely resulted in lower growth rate. This pattern suggests that there is an effect of temperature on growth rates of larval suckers, but GDD is likely a more effective metric when used only on a single cohort of larvae.

Relationship between GDD and growth rate may also have been influenced by the method by which GDD was calculated. Due to drying in sampled habitat, temperature loggers were stranded so mean daily water temperature was recorded from a main channel gage. Although temperature measured at the Bluff, UT gage accurately represented seasonal temperature in the main channel of the San Juan River; temperatures at the individual larval collection sites likely varied and may have been warmer or cooler than main channel temperature. A better relationship between growth rate and GDD may have been observed if temperature measurements more closely matched that of the backwaters in which the larvae were collected. Backwaters are important nursery habitat for larval fishes due to low velocity and favorable temperatures and, depending on size and depth, mean backwater temperature may be warmer than the main channel temperature (Carter et al. 1985; Tyus 1991; Tyus and Haines 1991).

Previous studies have found that while Bluehead and Flannelmouth Suckers both spawn in spring and early summer, Flannelmouth Suckers spawn at cooler temperatures than Bluehead Suckers. In this study, Flannelmouth Suckers spawned about one month earlier than Bluehead Suckers. This study documented a nearly five-month spawning period, from March to July, when native suckers were spawning in the San Juan River with Flannelmouth Sucker spawning primarily occurring between March and May and Bluehead Sucker occurring in two periods, from April to May and from late June to July.

Carter et al. (1985) observed a 50 fold increase in backwater habitat during high flows in the Upper Colorado River Basin. In the San Juan River, backwater surface area is positively related to antecedent flow condition parameters, in particular, increased flow creates increased backwater surface area (Lamarra and Lamarra 2013). Targeting flow to hatch and spawn dates of fishes maximizes benefits to larval native fishes. Specifically, knowledge of spawning dates aids conservation of both species by ensuring that flows may be managed for the creation of nursery habitat when larval fishes will be present in the river, and backwater (nursery) habitat may be enhanced by high flow events.

Temperature is a cue for spawning of Bluehead and Flannelmouth Suckers (Bezzerides and Bestgen 2002). Flannelmouth Suckers in the San Juan River spawned at similar temperatures to other drainages while the minimum temperature at which Bluehead Suckers spawn in the San Juan River may be lower than previously recorded (Snyder and Muth 2004; Carman 2007). In this study, T_{base}, the temperature below which spawning does not occur in the calculation for GDD, was selected based on observed spawning temperatures from other studies (Snyder and Muth 2004; Carman 2007); however, five Bluehead Sucker spawning dates occurred at zero GDD. Because cumulative GDD calculations do not begin until water temperature reaches T_{base}, it is possible that some spawning may have occurred at temperatures lower than the estimated T_{base}, 15°C. Characterizing the relationship between physiological processes and GDD explores the impact of the thermal conditions of a growing season rather than a particular time or temperature and is useful for analyzing temperature trends temporally and across drainages. As a result, although spawning dates may change annually as a result of a warmer or cooler growing season, the relationship between the onset of spawning and GDD should remain constant.

The San Juan River is a dam regulated system and receives most of its flow from the Animas River and discharge from Navajo Dam. Temperature in the San Juan River is influenced by a number of factors, including cold-water release from Navajo Dam, flow from the Animas River, and seasonal storm events (Miller and Swaim 2013). Water temperature is negatively correlated with flow, and temperature suppression is particularly exacerbated by extended cold-water releases from Navajo Dam in low flow years (Bliesner and Westfall 2010). Cold-water discharge from Navajo Dam can reduce the temperature of the river as far as Mexican Hat, Utah, a distance of 173 RM (Miller and Swaim 2013). Depending on flow conditions and source of flow, temperature in the San Juan River may vary from year to year. Many physiological processes are temperature-regulated, so cold-water releases from the dam may delay spawning by native suckers and slow incubation times and growth rates; however, depending on the magnitude of the release, releases from Navajo Dam may also be imperative for creation of nursery habitat for larval fishes.

Spawning periodicity, growth rate, and hatch dates are all mediated by water temperature both in the main channel and nursery habitats. Suitable flow and temperature in main channel and backwater habitats are essential for the survival of both species, and changes to the thermal regime of the San Juan River which result in cooler temperatures may threaten these species. Conversely, warmer temperatures increase metabolic rates which result in accelerated incubation times, increased hatch rates, and increased growth rates, which are all advantageous for survival (Bozek et al. 1990; Bestgen 2008). However, while not determined for Bluehead or Flannelmouth Suckers, there is likely an upper thermal limit at which temperature becomes harmful or lethal for both species (Carman 2007). The San Juan River, like many rivers, is dam regulated and subject to both flow and thermal modifications. Knowledge of native fishes' needs allows dam operations to proceed in a way that benefits native fishes and enhances survival.

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