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Predicted and Observed Responses of a Nonnative Channel Catfish Population Following Managed Removal to Aid the Recovery of Endangered Fishes

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Abstract

Human transformation of aquatic systems and the introduction of nonnative species increasingly threaten the persistence of imperiled freshwater fishes. In response, large-scale mechanical removal of nonnative fishes has been implemented throughout parts of the Colorado River basin to aid recovery of endangered fishes, but the effects of these efforts can be difficult to quantify. Fisheries population models for predicting outcomes of harvest regulations have been widely used to prevent overfishing of commercial and game stocks. Here, we used population models to investigate size-specific removal efforts needed to overfish a nonnative population of Channel Catfish *Ictalurus punctatus* and thereby aid recovery of endangered fishes in the San Juan River, New Mexico and Utah. The minimum size of fish that were efficiently captured with electrofishing gear was 280 mm TL, and annual removal rates increased with fish size, ranging from 0.10 for 200-mm fish to 0.44 for 600-mm fish. Model results suggested that removal rates should be increased from 0.14 to a range of 0.21–0.34 to cause growth overfishing and should be increased to a range of 0.26–0.29 to cause recruitment overfishing at a minimum electrofishing size limit of 280 mm TL. However, model results indicated that overall population abundance and biomass are being substantially reduced compared to an unmanaged population. In concordance, long-term monitoring data from 1991 to 2015 demonstrated a decrease in Channel Catfish TL and mass as well as an increase in catch rate variability since removal efforts intensified in 2006. Overall, current rates of removal will probably not achieve collapse of the nonnative Channel Catfish population in the San Juan River, but the reduction in size structure indicates that the population has responded to these efforts.

Freshwater fishes are threatened across the globe by the spread of nonnative species (Miller et al. 1989; Dextrase and Mandrak 2006; Dudgeon et al. 2006; Jelks et al. 2008), and invasive fishes are now prevalent in most North American basins (Gido and Brown 1999). Ecological and evolutionary effects of nonnative species on native fishes have been well documented and can occur at several levels of biotic organization (Strayer 2010; Cucherousset and Olden 2011). As a result, native fishes can suffer declines through competition with or predation by nonnative species (Minckley and Deacon 1968; Mills et al. 2004; Strayer 2010). Naturally depauperate fish communities, like those found in the American Southwest, are especially vulnerable to nonnative fish invasion and establishment (Fitzgerald et al. 2016), which has led to unprecedented imperilment of endemic fishes in this region (Minckley and Deacon 1968).

Efforts to control or eradicate problematic nonnative fishes can be relatively inefficient because of limited ability to substantially reduce population sizes using common fisheries techniques (Mueller 2005; Coggins et al. 2011; Franssen et al. 2014; Propst et al. 2015). Nonetheless, these mechanical removal efforts have been implemented across the Colorado River basin and are among the few options managers have to suppress nonnative fishes (Tyus and Saunders 1996, 2000; USFWS 2002). Despite extensive and continued use of nonnative removal efforts, there has been limited documented success in these systems (Mueller 2005), largely due to the difficulty in linking population changes to these management actions over large spatial and temporal scales (Franssen et al. 2014; Propst et al. 2015).

Outcomes of mechanical removal efforts aimed at reducing nonnative species are highly variable (Meronek et al. 1996), and it has generally been difficult to measure

responses in both target and non-target populations. Fisheries population models can be used to monitor and assess exploited fish populations (Ricker 1975), and typically these models are used to predict the outcome of proposed harvest regulations on exploited fisheries, with the goal of preventing overfishing (Allen and Hightower 2010; Eder et al. 2016). Contrary to goals of managing recreational or commercial fisheries, nonnative fish removal programs seek to reduce the size of target populations and, ideally, cause their collapse to aid native species. However, the use of fisheries population models to estimate efforts of purposeful population depletions has been rare (Weber et al. 2011; Tsehaye et al. 2013).

Mechanical removal of nonnative fishes in the San Juan River, New Mexico and Utah, has been ongoing since the late 1990s, with variable effort and spatial coverage, to aid endangered fishes (Franssen et al. 2014). Removal efforts have focused primarily on Channel Catfish *Ictalurus punctatus* and Common Carp *Cyprinus carpio*, with the latter being effectively reduced in number over time; however, Channel Catfish remain relatively abundant in the system (Franssen et al. 2014). Because these removal efforts are both costly and time consuming, there is a need to evaluate their effectiveness and continued feasibility of reducing targeted nonnative Channel Catfish.

Here, we used fisheries population models and standardized monitoring to investigate the effect of nonnative Channel Catfish removal efforts aimed at benefiting the recovery of the federally protected Colorado Pikeminnow *Ptychocheilus lucius* and Razorback Sucker *Xyrauchen texanus* in the San Juan River. To accomplish this, we (1) used field-collected data to quantify size-specific rates of Channel Catfish removal using mark–recapture; (2) used field-based and literature-derived data to parameterize population models for estimating the rates of size-

dependent removal required to attain growth overfishing and recruitment overfishing of the population; (3) calculated the predicted percent reduction in the total number of individuals and biomass under variable removal rates and size-selective removal limits; and (4) used long-term monitoring data to assess temporal trends in Channel Catfish population demographics that were likely impacted by size-selective removal.

METHODS

Study area.—The San Juan River flows out of southwest Colorado and through the high desert of New Mexico and Utah before joining the Colorado River at Lake Powell (Figure 1). The San Juan River was impounded in 1962 by Navajo Dam, resulting in a drastically altered flow and temperature regime (Franssen et al. 2007). Since impoundment, mean annual discharge has been reduced by 23% (U.S. Geological Survey gauging station 09368000), and hypolimnetic releases from the dam decrease water temperature and create a longitudinal gradient in the river's thermal regime (Ryden and Ahlm 1996; Miller and Swaim 2013; Franssen and Durst 2014). The river was demarcated into river kilometers (rkm), where rkm 0.0 is located near the inflow to Lake Powell, and the rkm increases upstream

toward Navajo Dam (rkm 362.1). The river demonstrates longitudinal variation in abiotic and biotic characteristics: in upstream reaches, the river's floodplain allows for channel meandering and braiding, but near rkm 109.4, canyons constrain the river channel until it enters Lake Powell. Additionally, in-channel habitat has been simplified by riverwide establishment of nonnative salt cedar *Tamarix* spp. and Russian olive *Elaeagnus angustifolia*. Portions of the native fish community remain intact, with native suckers (Catostomidae) demonstrating greatest densities in upstream reaches, while nonnative Channel Catfish have greater densities downstream (Franssen et al. 2016). Age structure and size structure of Channel Catfish also vary longitudinally; greater densities of larger, older fish occur in upstream reaches, and smaller, younger fish are more common in downstream reaches (Franssen et al. 2016).

Channel Catfish removal and size selectivity.—We estimated size-specific Channel Catfish removal rates between 2011 and 2015 from fish that were marked and recaptured during electrofishing efforts that included nonnative removal efforts and standardized fish community monitoring (see Franssen et al. 2014 for more details on removal efforts). Channel Catfish were collected using raft-mounted electrofishing units (Smith-Root 5.0 GPP, Smith-Root, Vancouver, Washington; or ETS MBS-1DP-

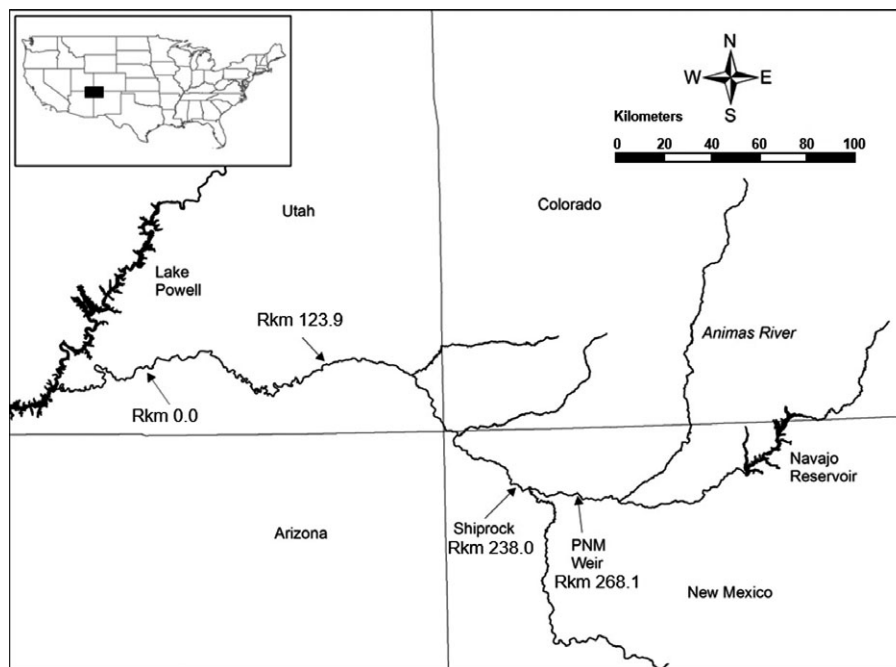


FIGURE 1. Study area of the San Juan River, where predicted effects of removal on Channel Catfish were investigated. Nonnative fish removal has occurred with varying degrees over time between river kilometer (rkm) 268.1 (Public Service Company of New Mexico [PNM] Weir; impassible to fish at base flows) and rkm 0.0. Channel Catfish were tagged between rkm 238.0 (Shiprock, New Mexico) and rkm 4.7 during 2011–2015 to assess removal rates. Subsequent removal passes occurred from rkm 238.0 to rkm 4.7 in all years except 2015, when efforts were limited to between rkm 255.2 and rkm 4.7. Channel Catfish were also removed during fall monitoring efforts from rkm 289.7 to rkm 85.3, except in 2015, when sampling extended downstream to rkm 4.7.

TABLE 1. Numbers and size-classes of Channel Catfish tagged annually to quantify size-specific removal rates in the San Juan River between 2011 and 2015.

TL (mm)	2011	2012	2013	2014	2015
201–250	546	1,244	251	115	193
251–300	1,073	1,071	1,121	377	760
301–350	550	509	679	666	991
351–400	272	269	260	800	703
401–450	232	221	156	425	444
451–500	159	157	96	215	175
501–550	100	112	53	114	58
551–600	34	34	24	56	38
601+	12	18	14	22	22

RLY-COS, ETS Electrofishing Systems, Madison, Wisconsin) from spring (March or April) through fall (September or October). Each year started with a downstream collection pass between rkm 238.0 and rkm 4.7 to mark Channel Catfish before initiation of further recapture passes to quantify removal rates. During a single pass (with a pair of electrofishing rafts, each sampling opposite river banks perpendicular to shore), Channel Catfish were captured, marked with an individually labeled T-bar anchor tag (Floy Tag, Seattle), measured for TL to the nearest millimeter (only Channel Catfish > 200 mm TL were marked), and returned to the river (range = 2,654–3,635 individuals tagged annually; Table 1). During subsequent removal passes, Channel Catfish were recaptured, and all individuals (marked and unmarked) were removed from the river between rkm 268.1 and rkm 4.7 (in 2015, removal efforts were limited to between rkm 255.2 and rkm 4.7). Additional removal of Channel Catfish occurred during standardized community monitoring between rkm 289.7 and rkm 85.3 in all years except 2015, when sampling was extended downstream to rkm 4.7.

From these mark–recapture efforts, we estimated annual and overall size-specific removal rates by quantifying the probability of recapture over the size range of tagged fish. We first quantified annual variability of size-specific removal rates by conducting five separate logistic regression models predicting the probability of recapture by size of fish tagged in each year. Because all Channel Catfish were removed after the first marking pass of each year, only within-year recaptures were included in removal rate estimates. To estimate mean overall size-specific removal rates, we used a generalized mixed-effects model (binomial) with the “glmer” function in the lme4 package (Bates et al. 2015) to predict the probability of recapture for tagged Channel Catfish, with size (TL) as a fixed factor and year as a random effect. The use of a mixed-effects model allowed us to quantify the probability of

recapture along a continuous fixed effect (in this case, TL), while the use of year as a random effect included annual variability in our estimates but avoided disproportionate effects on model estimates due to variable sample sizes among years. Models and 95% confidence intervals of parameter estimates (“confint” function) were generated using the R statistical language (R Core Team 2015).

The use of mark–recapture methods often assumes that the proportion of marked fish recaptured is equivalent to the proportion of marked fish in the population (Ricker 1975). However, factors such as unreported tag recovery, mortality, emigration, or effects of marking on susceptibility to recapture could violate this assumption. We believe that these factors were likely minimal in our study because of low incidences of T-bar tag loss reported in Channel Catfish (Buckmeier and Irwin 2000), and unreported tag recovery from recreational or commercial fishing was minimal, as the majority of the San Juan River is located in remote areas with extremely low recreational fishing pressure and no commercial fishing. Moreover, emigration of tagged individuals was potentially limited due to few permanent tributaries and an upstream barrier (impassible weir at rkm 268.1). Additionally, mortality was minimized by the relatively short duration of removal in each year (~6 months). Nevertheless, all of these factors could have biased our removal estimates downward; therefore, our estimates should be considered conservative.

Because fisheries population models often evaluate size limit restrictions to harvest, we similarly needed to identify the minimum size of Channel Catfish that could be effectively captured using electrofishing (hereafter, “minimum electrofishing size limit”). We interpreted this lower bound as the cutoff at which increased effort would likely not increase removal rates due to inefficiency of capture. To estimate the minimum electrofishing size limit, we used a length-frequency distribution of all Channel Catfish captured during the marking pass in each year. Assuming a declining total abundance of individuals as fish grow, we estimated the minimum electrofishing size limit of Channel Catfish as the mode of fish captured among all sizes.

Population modeling.— Fisheries population models are often used to assess the effects of fishing exploitation (recreational and commercial) on target populations, but fishing exploitation of Channel Catfish is extremely low in the San Juan River, and nonnative fish removal is arguably different than fishing exploitation in the traditional sense. However, because exploitation and removal rates can be functionally treated the same in these population models (i.e., as annual size-specific mortality rates), we substitute the term “exploitation” with the term “removal” for clarity, when appropriate.

We modeled the predicted effects of removal on the Channel Catfish population in the San Juan River by using the Fishery Analysis and Modeling Simulator (FAMS;

Slipke and Maceina 2013). The FAMS software provides a user-friendly interface to populate the Beverton–Holt equilibrium yield model and allows the modeling of population responses to different minimum size limits and rates of removal (size-specific removal rates in our case). Specifically, we used the yield-per-recruit model (a single-cohort, length-based model) to investigate rates of size-dependent removal that were predicted to overfish the population by growth and recruitment (Slipke and Maceina 2013). Second, we used the dynamic pool model (a multi-cohort, age-structured model with constant recruitment) to assess the predicted percent reduction in total number of individuals and biomass of the population under different removal and minimum length limit scenarios (or size-specific removal rates). It should be noted that these models assume no density dependence dynamics or compensatory responses in recruitment, growth, or mortality rates; furthermore, they do not account for any potential population crashes in response to removal (Slipke and Maceina 2013).

We used life history and demographic data collected from Channel Catfish in the San Juan River when available and literature-derived sources otherwise to inform the models (Table 2). We estimated a length–weight relationship from Channel Catfish collected during standardized monitoring between 1991 and 2015 ($n = 4,980$; Appendix Figure A.1). Length at age (Appendix Figure A.2), von Bertalanffy growth parameters, and maximum age were estimated from pectoral spines of known-length Channel Catfish collected from the San Juan River ($n = 103$ [Farokhkish 2012]; along with 39 fish we collected in 2014). Spines were sectioned distal to the basal groove (Quist et al. 2012) with an IsoMet Low-Speed Saw (Buehler, Lake Bluff, Illinois) and were photographed under a dissecting microscope. Four

individuals independently aged pectoral spines from each fish by counting annual growth rings, and any discrepancies were rectified in concert. The maximum age of Channel Catfish was set as the oldest observed fish in the data set (15 years), and the maximum size (asymptotic length [L]) was set at 810 mm TL (the largest known Channel Catfish captured in the San Juan River). Because natural mortality rates of Channel Catfish in the San Juan River were unknown, we used a range of estimated conditional natural mortality rates (m ; i.e., 0.15, 0.20, and 0.25; from Simco and Cross 1966; Railbey and Jahn 1991; and Slipke et al. 2002; respectively). We assumed that females made up 50% of the population (Slipke et al. 2002), age at sexual maturity was 3 years (Helms 1975), and the percentage of females that spawned annually was 10% for age 3, 50% for age 4, and 75% for age 5 and older (Helms 1975). The relationship between fecundity and size of females in the San Juan River was obtained from Morel (2010).

Yield-per-recruit model.—We used the yield-per-recruit model to identify size-dependent removal rates that were predicted to result in growth overfishing or recruitment overfishing. We primed the model with 1,000 recruits, varied levels of removal (i.e., conditional fishing mortality [cf] = 0.00–0.90), and minimum length limits (100–500 mm TL). We modeled three different scenarios by varying m at 0.15, 0.20, and 0.25. Because we were primarily interested in the relative effects of removal rather than absolute metrics (e.g., total yield or relative number of eggs produced), we focused our analyses on relative yield and spawning potential ratio (SPR) values. The SPR quantifies the relative reduction in lifetime egg production of an average recruit in a fished population versus an unfished population (Goodyear 1993). We first quantified

TABLE 2. Parameters used in population models to assess the effects of mechanical removal on the nonnative Channel Catfish population in the San Juan River (L = asymptotic length; K = growth coefficient; t_0 = theoretical age at zero length). Sources of data are denoted with footnotes. Asterisks indicate parameter estimates that were derived from the San Juan River population.

Parameter	Value
von Bertalanffy growth function parameters ^{a*}	$L = 810$ mm; $K = 0.089$; $t_0 = -2.378$ years
Maximum age ^{a*}	15 years
Age at sexual maturation ^b	3 years
Length–weight relationship ^{c*}	$\text{Log}_{10}(\text{weight}) = [\text{log}_{10}(\text{length}) \times 3.349] - 5.959$
Conditional natural mortality ^d	0.15, 0.20, 0.25
Length–fecundity relationship ^{c*}	$\text{Log}_{10}(\text{fecundity}) = [\text{log}_{10}(\text{length}) \times 2.443] - 2.318$
Percentage of fish that are females ^d	50%
Percentage of females that spawn annually ^b	10% for age 3; 50% for age 4; 75% for age 5+

^aFarokhkish 2012; our unpublished data.

^bHelms 1975.

^cOur unpublished data.

^dSimco and Cross 1966; Railbey and Jahn 1991; Slipke et al. 2002.

^eMorel 2010.

predicted yield and SPR for all combinations of minimum length limits and removal rates and then identified growth overfishing as combinations where yield was lowered after reaching maximum sustained yield for each given combination. Similarly, we identified all combinations of minimum length limits and removal rates that decreased SPR below 0.20 (i.e., the value thought to elicit recruitment overfishing for Channel Catfish; Slipke et al. 2002). We compared estimated annual rates of size-dependent removal to those that were predicted to achieve growth overfishing or recruitment overfishing of the population.

Dynamic pool model.—We used the dynamic pool model to investigate predicted changes to the number of individuals, total biomass, and distribution of biomass among age-classes of Channel Catfish with varying rates of removal, minimum length limits, and natural mortality rates. Because this dynamic pool model is an age-based model, we assessed variation in removal rates by age-class rather than by size. Although we did estimate size-specific removal rates (see Results below), we did not vary removal rates among age-classes (i.e., removal rates were constant among age-classes in each modeled scenario) so as to be consistent with output from the yield-per-recruit model detailed above. We fixed annual recruitment at 1,000 individuals and primed the model with cm values of 0.15, 0.20, and 0.25. We allowed sufficient time steps for the model to reach a stable age distribution (15 years, the maximum age). We then calculated the predicted percent reduction in total numbers and biomass of Channel Catfish for the modeled population (with removal) compared to a modeled unmanaged population (without removal). We plotted the percent reduction in total numbers and biomass over different combinations of minimum length limits (i.e., mean length at age) and removal rates as isoclines. The observed rates of size-dependent removal were then plotted for comparison with modeled results. From these same model runs, we also quantified the predicted biomass distribution among three stable age-classes (i.e., ages 1, 2, and 3) using the mean lengths at age. We set removal rates (i.e., cf) from 0.00 to 0.40 at 0.10 increments, and these rates remained constant for all ages in each scenario.

Observed temporal variation in the Channel Catfish population.—Standardized monitoring of the large-bodied fish community has taken place on the San Juan River each fall since 1991 (using the same raft-mounted methodology previously described for removal efforts). Removal of Channel Catfish during these efforts first started in 1995. To assess any temporal trends in the Channel Catfish population, we quantified the total number of Channel Catfish removed each year across all efforts and compared those values to the observed Channel Catfish CPUE from standardized monitoring each fall (see

Franssen et al. 2016). We also quantified length and mass of Channel Catfish collected from standardized monitoring in the same season of each year to assess changes in the size and biomass structure of the population over time. Based on the scaling relationship between length and mass, we would expect changes in mass to be stronger than changes in length. To investigate temporal trends in these size metrics, we conducted quantile regressions at the 50th, 75th, and 95th percentiles of both TL and mass of Channel Catfish individuals as dependent variables and with time (year) as the predictor variable. Quantile regression was conducted using the “rq” function from the R package “quantreg” (Koenker 2015).

RESULTS

Channel Catfish Removal and Size Selectivity

Between 2011 and 2015, annual removal efforts averaged 1,045 h (range = 953–1,114 h) of electrofishing. We tagged a total of 15,441 Channel Catfish during marking passes, and 2,779 individuals were recaptured during subsequent removal passes (Table 1). Overall, the annual proportion of fish recaptured was higher for larger fish compared to the total proportion of tagged fish (Figure 2A). In concordance, estimated annual removal rates were lower—but generally similar over time—for smaller size-classes (<350 mm TL), whereas they increased and became more variable for larger size-classes (Figure 2B). Size-specific removal rates estimated from all years showed similar patterns, with mean estimated rates ranging from 0.10 for 200-mm fish to 0.44 for 600-mm fish; however, uncertainty in these estimates also increased for larger size-classes.

The length-frequency distribution of Channel Catfish captured during marking passes showed sharp declines at smaller size-classes, demonstrating reduced efficiency of capture (Figure 3). The mode was 280 mm TL, which was the minimum size of Channel Catfish we considered to be efficiently captured by electrofishing (i.e., the minimum electrofishing size limit); the estimated mean removal rate at this size was 0.14 (Figure 2B).

Yield-Per-Recruit Model

Model results suggested that minimum electrofishing size limits and removal rates predicted to elicit either growth overfishing or recruitment overfishing were generally similar (Figure 4). Variability in conditional mortality had stronger effects on the ability to growth overfish compared to recruitment overfish the population. Growth overfishing was predicted to occur with most combinations of removal rates above 0.16 (at 200 mm TL, cm = 0.15) and minimum electrofishing size limits less than 385 mm TL (i.e., largest minimum

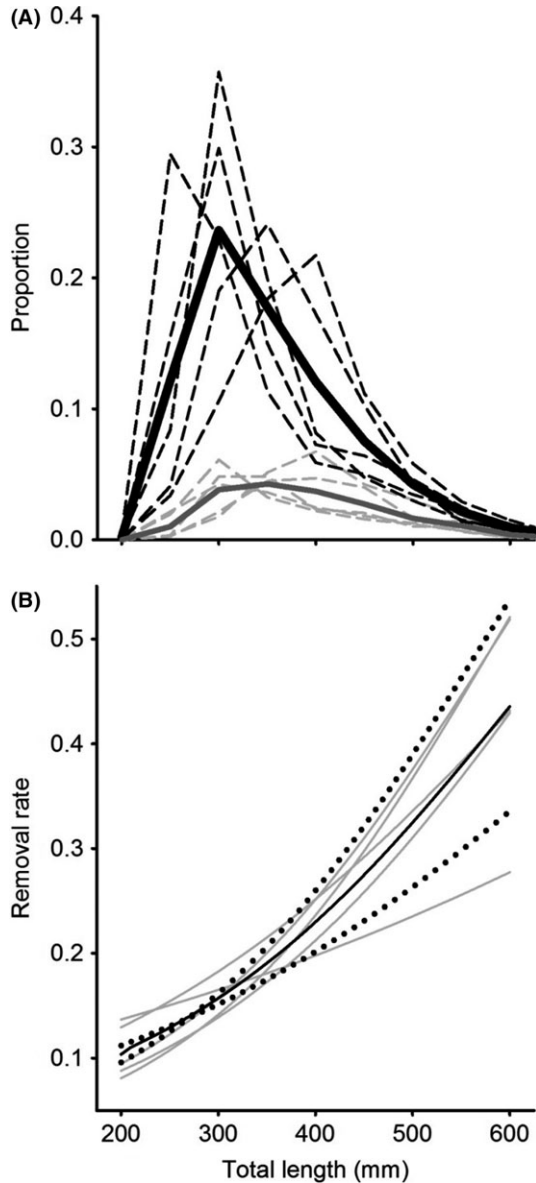


FIGURE 2. (A) Proportion of Channel Catfish that were tagged (black lines) and recaptured (gray lines) annually by size-class (dashed lines = yearly values; solid lines = mean across years); and (B) estimated size-dependent removal rate observed each year (gray lines are from logistic regressions; solid black line = estimated mean removal rate across years, from the mixed-effects model; dotted black lines = 95% confidence interval).

size limit of fish removed to elicit growth overfishing at $cm = 0.25$). However, estimated removal rates of fish smaller than 385 mm TL were likely not high enough at those sizes to cause growth overfishing in the population. At the minimum electrofishing size limit we observed (i.e., 280 mm TL), mean estimated removal rates (cf) would have to be increased from 0.14 to 0.21, 0.25, and 0.34 (at $cm = 0.15$, 0.20, and 0.25,

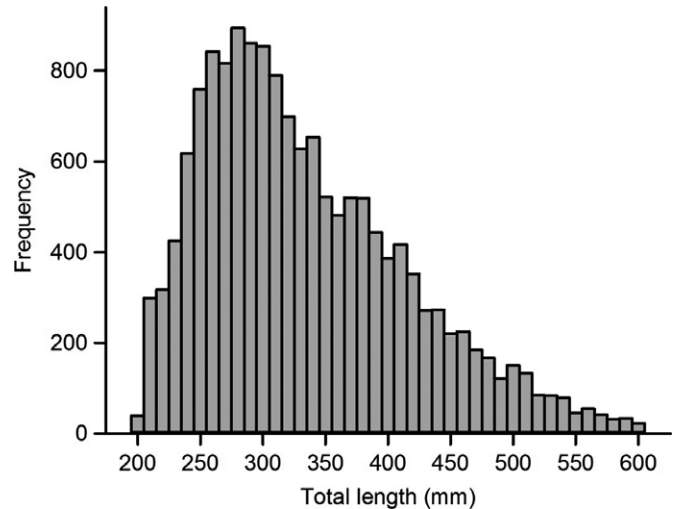


FIGURE 3. Length-frequency histogram of Channel Catfish collected during the marking pass for removal rate estimates from efforts on the San Juan River between 2011 and 2015. The minimum size that was efficiently removed was estimated as the mode (280 mm TL).

respectively) before growth overfishing would be predicted to occur in this population.

Similar to growth overfishing, small minimum electrofishing size limits and relatively high removal rates were predicted to result in recruitment overfishing (Figure 4). No removal rates with a minimum electrofishing size limit of 415 mm TL or greater (at $cm = 0.15$) would be predicted to result in recruitment overfishing, while a removal rate of at least 0.20 would be needed if the minimum electrofishing size limit was reduced to 200 mm TL (at $cm = 0.15$). Removal rates would also have to be increased if considering higher natural mortality rates (i.e., $cm = 0.20$ or 0.25). Estimated removal rates suggested that current levels of removal among size-classes are not likely to cause recruitment overfishing in the population. At the observed minimum electrofishing size limit (280 mm TL), mean estimated removal rates would have to be increased on average from 0.14 to 0.26, 0.26, and 0.29 (at $cm = 0.15$, 0.20, and 0.25, respectively) before recruitment overfishing would be predicted to occur.

Dynamic Pool Model

At the minimum electrofishing size limit (280 mm TL) and an estimated mean removal rate of 0.14, the dynamic pool model predicted a reduction in the number of individuals in the population by approximately 40% and a decrease in the total biomass by over 60% compared to an unmanaged population (Figure 5). At a given minimum removal size, removal rate, and natural mortality rate, results from the dynamic pool model indicated a greater reduction in total biomass of the population compared to total numbers of individuals. Variation in isoclines for

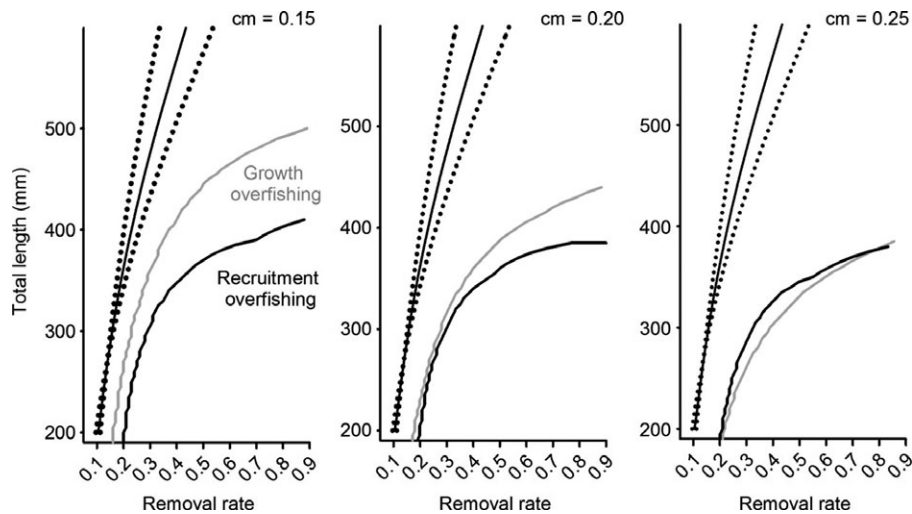


FIGURE 4. Predicted combinations of Channel Catfish removal rates and minimum electrofishing size limits at three levels of conditional natural mortality (cm) that would result in growth overfishing (gray line) and recruitment overfishing (black line) as well as the estimated mean rate (solid black line; dotted black lines represent 95% confidence intervals) of size-dependent removal between 2011 and 2015 in the San Juan River (see Figure 2B). Areas to the right of the gray line indicate removal rates and minimum size combinations that would reduce biomass yield past maximum sustained yields (i.e., growth overfishing). Areas to the right of the black line indicate conditions that are predicted to reduce the spawning potential ratio below 0.20 (i.e., recruitment overfishing).

both total number of individuals and biomass suggested that changes in removal rates of smaller fish would have a relatively strong effect on the population compared to larger fish.

The dynamic pool model indicated that even low levels of removal would exert strong impacts on the distribution of total biomass among age-classes of Channel Catfish (Figure 6). Not surprisingly, both increasing the capture of smaller fish (i.e., ages 1 and 2) and increasing the removal rate shifted the biomass to younger age-classes compared to an unmanaged population. However, variation in removal rates had stronger effects on the distribution of biomass compared to variation in minimum electrofishing size limits (mean TL = 210 mm at age 1; 260 mm at age 2; and 308 mm at age 3).

Observed Temporal Variation in the Channel Catfish Population

The total number of Channel Catfish removed from the San Juan River each year generally increased since 1991; sharp increases coincided with (1) the implementation of Channel Catfish removal during standardized monitoring in 1995, (2) initiation of targeted Channel Catfish removal in upstream reaches during 2001, and (3) expansion to nearly riverwide removal efforts starting in 2006 (Figure 7). The CPUE of Channel Catfish during standardized monitoring was variable over this time period, with no obvious temporal trends; however, the seven highest annual CPUEs occurred after intensive nonnative fish removal began in 2006. Additionally, both the total number of Channel Catfish removed across all efforts and the

CPUE during standardized monitoring were more variable over the most recent 10 years of the data set (coefficient of variation [CV] in CPUE = 45%; 2006–2015) compared to the period before intensive nonnative removal efforts began (CV = 37%; 1991–2005).

The observed size structure of the Channel Catfish population in the San Juan River demonstrated temporal trends between 1991 and 2015 (Table 3). Quantile regressions of the 50th, 75th, and 95th percentiles showed significant decreases in length and mass of captured Channel Catfish over time (all $P < 0.001$; Figure 7). As expected based on the scaling relationship between length and mass, the mass of individuals demonstrated much stronger declines compared to length over the study period. From 1991 to 2015, the median TL of Channel Catfish decreased by 89 mm, and median mass decreased by 93 g.

DISCUSSION

We combined model outcomes with long-term monitoring data to predict and assess the effects of removal efforts on Channel Catfish in the San Juan River. Our results indicate that current removal rates from electrofishing are too low at all sizes observed to induce overfishing of the Channel Catfish population in this system. Mean removal rates among all size-classes of fish were generally lower than the exploitation rates that were thought to have caused overfishing in a commercial Channel Catfish fishery in the Mississippi River (Pitlo 1997). Slipke et al. (2002) estimated exploitation rates ranging between 0.45 and 0.82 for Channel Catfish in the upper Mississippi

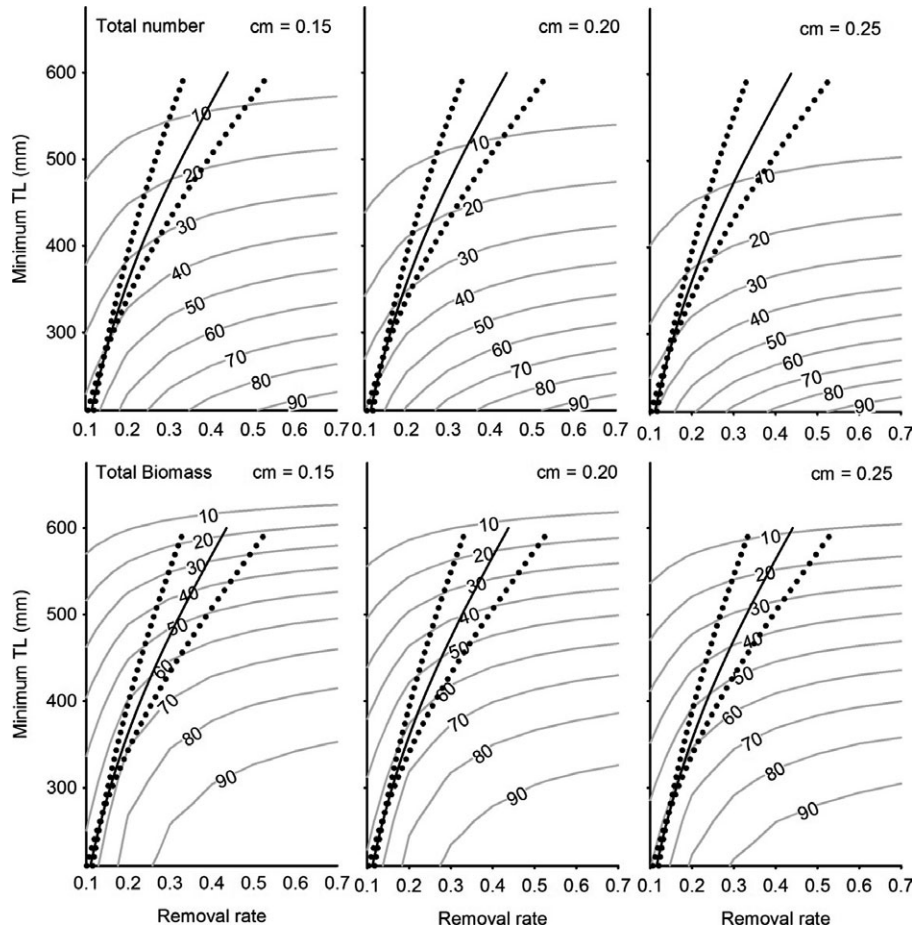


FIGURE 5. Predicted isoclines of the percent reduction in total number (top row) and biomass (bottom row) of Channel Catfish with varying rates of removal, modeled minimum electrofishing size limits, and conditional natural mortality (cm). Predicted percent declines were calculated from the difference between an unmanaged population and a population subjected to removal after the population reached equilibrium in each scenario. The estimated mean rate (solid black line; dotted black lines represent 95% confidence intervals) of size-dependent removal in the San Juan River between 2011 and 2015 is plotted for reference (see Figure 2B).

River, which caused a decline in commercial harvest due to overfishing. Modeled predictions from our study suggest that removal rates as low as 0.20 could elicit overfishing if smaller fish (i.e., ~200 mm TL) were efficiently removed, but this size was 80 mm TL smaller than our minimum electrofishing size limit. Relatively high removal rates necessary to overfish populations are commonly reported for other species targeted by managed removal efforts. For instance, high removal rates (>0.70) for a wide range of size-classes were predicted as necessary to elicit a crash in nonnative populations of Bighead Carp *Hypophthalmichthys nobilis* and Silver Carp *H. molitrix* in the Illinois River, Illinois (Tsehaye et al. 2013). Additionally, Haines and Modde (2007) predicted that removal rates exceeding 0.60 would be necessary to achieve a collapse in the nonnative Smallmouth Bass *Micropterus dolomieu* population in the Yampa River, Colorado. To date, the ability of managers to increase the removal rates of

Channel Catfish in the San Juan River has been restricted to increasing the number of electrofishing passes, and other methodologies that could increase the removal rates and improve the minimum electrofishing size limits have not been thoroughly investigated.

The benthic ecology and life history traits of Channel Catfish likely decrease their susceptibility to electrofishing compared to other invasive fishes. Male Channel Catfish excavate nests in cavities or undercut banks and guard the eggs until the larvae leave the nest (Hubert 1999), and their benthic habitat use makes them more difficult to see and net, especially in turbid water (Reynolds and Kolz 2012). This combination of reproductive strategy and habitat use likely makes Channel Catfish more resistant to electrofishing-based removal efforts. Other nonnative fishes, like the Common Carp, rely on floodplain habitat for successful spawning and tend to be highly susceptible to electrofishing (Stuart and Jones 2006; Jones and Stuart

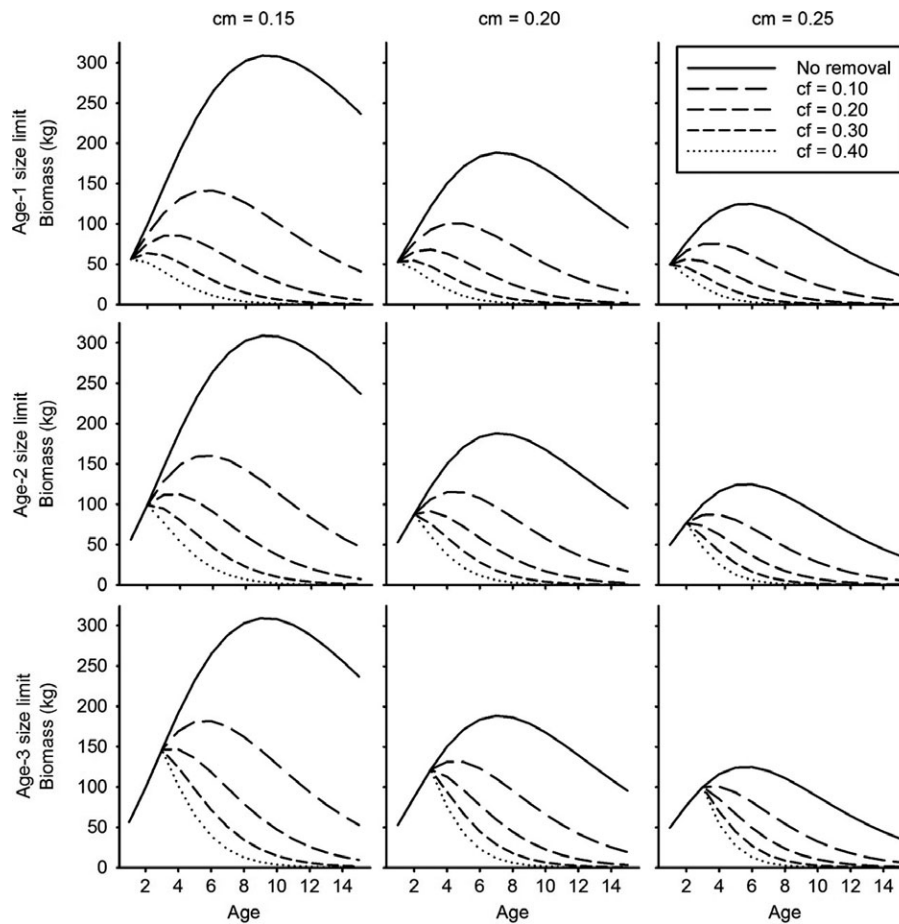


FIGURE 6. Predicted biomass distribution among age-classes of a Channel Catfish population under three modeled minimum electrofishing size limits (i.e., predicted mean length = 210 mm TL at age 1; 260 mm at age 2; and 308 mm at age 3; separate panels) with varying levels of removal (conditional fishing mortality [cf]) and conditional natural mortality (cm).

2008), which likely contributed to their decline after removal efforts in the San Juan River (Franssen et al. 2014). However, the combined use of electrofishing with other sampling gear could increase Channel Catfish removal rates. Eder et al. (2016) used 24-h baited hoop nets for Channel Catfish in the Missouri River, Nebraska, with estimated exploitation rates ranging from 0.18 to 0.41. The effectiveness of hoop nets can vary, as the choice of bait and mesh sizes affect which species and size distributions are captured (Pierce et al. 1981; Holland and Peters 1992; Buckmeier and Schlechte 2009). This passive capture method could be used to supplement current electrofishing methods that only effectively capture fish larger than 280 mm TL, but it is currently unclear whether the use of hoop nets would improve economic efficiency of Channel Catfish removal in the San Juan River.

Although current removal rates are not likely to cause a collapse of the Channel Catfish population in the San Juan River, our results suggest that the amount of fish biomass has been reduced substantially due to removal of

larger, older fish compared to an unmanaged population. This overall reduction in biomass and size-dependent selection of Channel Catfish may reduce intraspecific competition and alter selection pressures on the population, which could lead to maturation at younger ages and an increased number of smaller-sized fish (Ricker 1981; Fenberg and Roy 2008). This would have unintended consequences for endangered fishes in the San Juan River if small Channel Catfish compete with or prey upon young life stages of endangered fishes. Competition has been documented between nonnative and native fishes (e.g., Colorado Pikeminnow; Karp and Tyus 1990), but in the San Juan River, deleterious interactions of nonnative Channel Catfish with native fishes (other than as a choking hazard for native predators; Ryden and Smith 2002) have not been empirically demonstrated (Franssen et al. 2014). Elsewhere, Channel Catfish can prey on young life stages of endangered fishes (Tyus and Saunders 1996), but comprehensive knowledge on additional effects of Channel

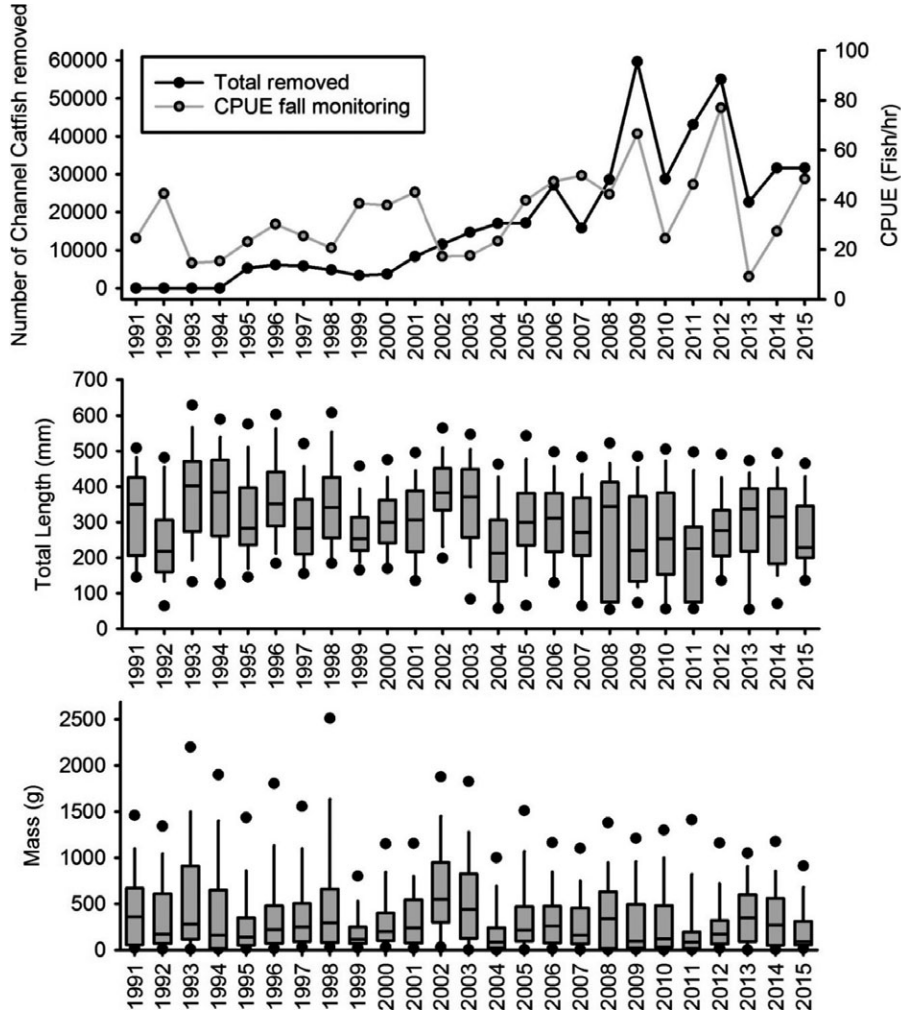


FIGURE 7. The total number removed and CPUE of Channel Catfish from fall monitoring surveys conducted in the San Juan River between 1991 and 2015 (top panel). Box plots of observed Channel Catfish TL (middle panel) and mass (bottom panel) from standardized monitoring surveys between 1991 and 2015 are also shown. In the box plots, filled circles represent 95% and 5% quantiles, whiskers represent 85% and 15% quantiles, top and bottom edges of the box represent 75% and 25% quantiles, and the middle line represents the median.

TABLE 3. Results of quantile regressions testing for temporal trends in the 50th, 75th, and 95th percentiles of Channel Catfish TL (mm) and mass (g) in the San Juan River between 1991 and 2015 (CL = confidence limit).

Variable	Percentile	Intercept	Slope estimate	Upper 95% CL	Lower 95% CL	P-value
TL	50	338	-3.69	-4.14	-3.23	<0.001
	75	432	-3.29	-3.76	-2.81	<0.001
	95	592	-5.00	-5.79	-4.21	<0.001
Mass	50	226	-3.89	-4.83	-2.95	<0.001
	75	661	-11.43	-13.42	-9.44	<0.001
	95	1,792	-30.63	-37.34	-23.91	<0.001

Catfish on multiple life stages (including eggs) of endangered fishes is lacking.

Temporal variation in the size structure of Channel Catfish suggests that nonnative removal efforts have

induced effects on the Channel Catfish population in the San Juan River. Monitoring data demonstrate that the annual CPUE of Channel Catfish has become more variable since 2006, when intensive removal efforts began. We

suggest this amplified annual variability in CPUE is likely driven by the removal of larger, older individuals, which has resulted in an increased reliance on annual recruitment, leading to higher temporal variation in population size. Indeed, exploitation alone can cause increased population variability in fishes due to the removal of larger individuals from the population and can manifest without obvious declining trends in overall abundance (Hsieh et al. 2006). Increased population fluctuations as age structures become truncated are commonly regarded as cautionary evidence that overfishing is occurring in commercial fisheries (Hsieh et al. 2006, 2010; Anderson et al. 2008). Healthy populations of relatively long-lived fishes typically have heavy-tailed age structures, which can buffer the populations against stochastic environmental processes (Hsieh et al. 2010). Although trends in overall CPUE of Channel Catfish in the San Juan River have not exhibited declines, the reduced size structure and the elevated annual variability in CPUE suggest that current levels of removal could be applying stress to the population. Alternatively, removal efforts could be increasing recruitment rates of Channel Catfish if competition with older age-classes is being relaxed. Future investigations will likely be needed to identify the specific mechanisms behind these observed patterns.

With the continued proliferation of nonnative species in aquatic systems, the coming decades will be challenging for conservation biologists. Understanding the contribution of nonnative species as a threat to native species persistence relative to the threats posed by other anthropogenic stressors will be imperative for making informed management decisions. Our knowledge of interactions among all life stages of Channel Catfish and native fishes in the San Juan River is extremely limited. Nonetheless, nonnative fish removal via electrofishing has continued in this system under the guise of beneficial effects to native species and in the absence of other available management actions for reducing threats to native fishes (Franssen et al. 2014). Our results suggest that the current levels of Channel Catfish removal are causing measurable impacts to the population, but because electrofishing is generally size-selective for larger individuals, the persistence of this population is likely inevitable. Thus, goals of nonnative fish management will be limited to population suppression until more efficient strategies that reduce juvenile survival or lower the reproductive output of adults are identified and implemented.

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Appendix

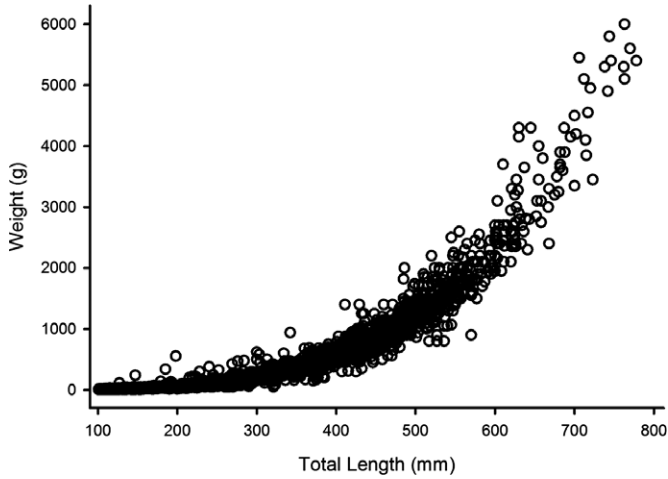


FIGURE A.1. Length-weight relationship for Channel Catfish in the San Juan River ($n = 4,980$).

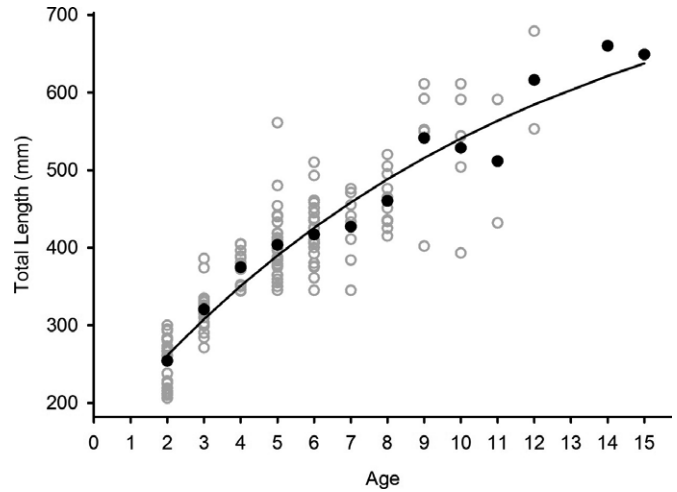


FIGURE A.2. Length-at-age relationship for Channel Catfish in the San Juan River. The open gray circles represent individuals, the filled circles represent mean size at each age, and the line is the fitted von Bertalanffy growth function, where length at age t (L_t) = $810 \cdot [1 - e^{-0.089(t + 2.378)}]$.