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Final Report

June 2014

Upper Colorado River Endangered Fish Recovery Program, Project 161

Bureau of Reclamation Agreement # 9-FC-81-0143 09FC402885

Larval Fish Laboratory Contribution 169

POPULATION TRENDS OF SMALLMOUTH BASS IN THE UPPER COLORADO RIVER BASIN WITH AN EVALUATION OF REMOVAL EFFECTS

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Upper Colorado River Endangered Fish Recovery Program

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Recovery Program Project #161

Bureau of Reclamation Agreement #9-FC-81-0143 09FC402885

Larval Fish Laboratory Contribution 168

June 2014

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Acknowledgements

The Recovery Program is a joint effort of the U.S. Fish and Wildlife Service, U.S. Bureau of Reclamation, Western Area Power Administration, states of Colorado, Utah, and Wyoming, Upper Basin water users, environmental organizations, the Colorado River Energy Distributors Association, and the National Park Service. We are grateful for the insights provided by employees of the recovery program and their collaborators including P. Martinez, B. Wright, T. Jones, A. Webber and C. Walford. ARB extends a special thank you to the crews and Principal Investigators that he worked with during 2009 sampling trips in Little Yampa Canyon and Lily Park (J. Hawkins crew), Echo Park to Split Mountain and Yampa Canyon (T. Jones crew): K. Cornell, C. Smith, J. Doering, N. Berndt, E. Glenn, C. Heim, D. Tuttle, B. Kohler and A. Kellner. This study was funded by the Upper Colorado River Endangered Fish Recovery Program.

Suggested Citation: Breton, A. R, D. L. Winkelman, J. A. Hawkins, and K. R. Bestgen. 2014. Population trends of smallmouth bass in the upper Colorado River basin with an evaluation of removal effects. Final report to the Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado. Larval Fish Laboratory Contribution 169.

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Executive Summary

Smallmouth bass *Micropterus dolomieu* were rare in the upper Colorado River basin until the early 1990's when their abundance dramatically increased in the Yampa River sub-basin. Increased abundance was due primarily to colonization from Elkhead Reservoir, which was rapidly drawn down twice, first to make improvements to the dam (1992) and a second time for reservoir expansion (2005), and allowed escapement of resident bass to the river through an unscreened outlet. Elkhead Reservoir is located on Elkhead Creek, a tributary of the Yampa River. The rapid Elkhead Reservoir drawdown in 1992 was followed by a period of drought years with low, early runoff in the Yampa River sub-basin that benefitted smallmouth bass reproduction. This combination of factors allowed smallmouth bass to establish a self-sustaining population in the Yampa River. Subsequently, successful recruitment allowed smallmouth bass to disperse upstream and downstream in the Yampa River and eventually move into the downstream Green River. Smallmouth bass were also likely introduced, by unknown means, into the upper Colorado River and have since dispersed in this sub-basin. The rapid increase of smallmouth bass in the upper Colorado River basin overlapped with significant reductions in native fish populations in some locations. The threat to these native fishes initiated intensive mechanical removal of smallmouth bass by the Upper Colorado River Endangered Fish Recovery Program.

In general, three factors explain fluctuating patterns in smallmouth bass density in the upper Colorado River basin in the last decade: reductions due to electrofishing removal, bass recovery after exploitation due to recruitment and immigration, and changes due to environmental factors not related to electrofishing and other management actions. Our analyses indicated that smallmouth bass densities were substantially reduced in most years by

electrofishing removal efforts. Less often, but dramatically in some cases, environmental effects were also responsible for significant declines in smallmouth bass densities in some reaches. Abundant year classes of young smallmouth bass produced in low flow and warm years such as 2007 have potential to overwhelm removal efforts, and the year class persists for one or more years. Nonetheless, it appears that increased electrofishing removal efforts from 2007 to 2011 resulted in sustained reductions in density of smallmouth bass sub-adults and adults throughout the upper basin despite environmental conditions that favored smallmouth bass reproduction in some years (e.g. 2007 and 2009), subsequent recruitment into sub-adult and adult age classes, and movement of smallmouth bass which previously (prior to increases in electrofishing removal efforts) allowed densities to recover in some reaches.

We recommend that removal efforts continue in most areas of the upper basin but that the Recovery Program consider allocating effort based on population trends and suspected areas of highest smallmouth bass reproduction. For instance, reproduction, recruitment, and movement of smallmouth bass allowed densities to recover in some reaches, particularly Little Yampa Canyon. Smallmouth bass population recovery implies that areas such as Little Yampa Canyon itself or adjacent reaches (especially upstream), may provide important habitat for age-0 production. We recommend continued assessment of smallmouth bass populations in reaches where reproduction or age-1 nurseries are suspected, such as Little Yampa Canyon and the adjacent upstream reach. It may also be necessary to expand monitoring to areas surrounding suspected sources of smallmouth bass reproduction and increase electrofishing removal effort in these reaches.

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and fixing these parameters improved AIC_c model support. Marking was not always conducted on pass one as implied by recapture probabilities. Figures include symmetrical 95% confidence intervals.

Introduction

Introduction and establishment of non-native fish in rivers of the western United States is a major threat to native fish assemblages (Minckley and Deacon 1968; Stanford and Ward 1986; Moyle *et al.* 1986; Carlson and Muth 1989; Minckley and Deacon 1991; Olden *et al.* 2006; Coggins *et al.* 2011; Loppnow *et al.* 2013). In the upper Colorado River basin, non-native fish invasions began over 100 years ago, with introductions of channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, and various salmonids. In the 1960's, small-bodied fishes such as red shiner *Cyprinella lutrensis* were relatively rare in the Green River sub-basin of the upper Colorado River basin (Vanicek *et al.* 1970), but by the 1970's red shiner expanded rapidly (Holden and Stalnaker 1975a and 1975b; Olden *et al.* 2006) and are now a dominant species in low-velocity habitat used by early life stages of native fishes (Haines and Tyus 1990; Dunsmoor 1993; Ruppert *et al.* 1993; Muth and Snyder 1995; Bestgen *et al.* 2006a).

Large-bodied non-native species such as smallmouth bass *Micropterus dolomieu* were rare in the upper Colorado River basin prior to 1992. They were not detected by extensive Yampa River sampling in 1951, 1967–1971 and 1976–1977 (Bailey and Alberti 1952; Holden and Stalnaker 1975b; Carlson *et al.* 1979; Breton *et al.* 2013a). Only one individual was captured during extensive electrofishing sampling in the Yampa River from 1981–1982 (Hawkins *et al.* 2009; Wick *et al.* 1985), and similar efforts from 1986–1988 did not detect any bass (McAda *et al.* 1994). Smallmouth bass were introduced into the Yampa River basin when the Colorado Division of Wildlife (now Colorado Parks and Wildlife) stocked them in Elkhead Reservoir in 1978 (Hawkins *et al.* 2009; Breton *et al.* 2013a). A dramatic increase in smallmouth bass in the Yampa River began in the early 1990’s and now they comprise a major percentage of the fish community (McAda *et al.* 1994; Anderson 2004; Hawkins *et al.* 2009). Increased abundance was due primarily to smallmouth bass escapement from Elkhead Reservoir when the reservoir was rapidly drawn down to make improvements to the dam in1992 and for reservoir expansion in 2005 (Hawkins *et al.* 2009, Breton *et al*. 2013a), which allowed resident bass to escape downstream. Elkhead Reservoir spills into Elkhead Creek just a short distance upstream of its Yampa River confluence (Breton *et al.* 2013a). The drawdown of Elkhead Reservoir in 1992 was followed by a period of drought years with low, early runoff in the Yampa River sub-basin that benefitted smallmouth bass reproduction. This combination of factors allowed smallmouth bass to establish a self-sustaining population. Since the early 1990's, smallmouth bass and northern pike *Esox lucius* have established self-sustaining populations in the middle and lower Yampa River, the upper and middle Green River basins, and the upper Colorado River (Anderson 2002, 2005; Hawkins *et al.* 2005; Bestgen *et al.* 2006b; Hawkins *et al.* 2009).

The predatory threat of large-bodied piscivorous taxa such as smallmouth bass and northern pike is substantial. For example, results of a bioenergetics model (Johnson *et al.* 2008) ranked smallmouth bass as the most problematic invasive species in the upper Colorado River basin because of their high abundance, habitat use that overlaps with most native fishes, and ability to consume a wide variety of life stages of native fishes. In addition, expanded populations of piscivores such as smallmouth bass are a major impediment to conservation actions aimed at recovery efforts for four endangered fishes in the upper Colorado River basin: Colorado pikeminnow *Ptychocheilus lucius*; razorback sucker *Xyrauchen texanus*; humpback chub *Gila cypha*; and bonytail *Gila elegans* (U.S. Fish and Wildlife Service 2002a, b, c, d). In response to the predatory threat posed by non-native fishes such as smallmouth bass, by about 2004 the Upper Colorado River Endangered Fish Recovery Program (Recovery Program) and their collaborators had initiated efforts in earnest to control such species via mechanical removal in affected reaches (U.S. Fish and Wildlife Service 2004; Chart *et al.* 2008; Hawkins *et al.* 2009).

This report summarizes removal efforts and smallmouth bass density trends in the upper Colorado River basin from 2001–2011. Our results and conclusions apply only to environmental conditions that were present during the study, especially conditions from 2004 to 2011 (years of our abundance analysis, more below). Above and below, we refer, in particular, to environmental conditions that did or did not favor smallmouth bass reproduction and age-0 (YOY) overwinter survival – key demographic parameters for the sampled population. Despite the duration of the available time series and considerable variation in environmental conditions over this period, we suggest caution when making inferences to years and locations not included in our analyses. Our goal was to quantitatively assess smallmouth bass population trends in the Yampa, Green, White, Gunnison, and Colorado River sub-basins of the upper Colorado River basin. Our analysis consists of two parts: (1) a descriptive summary of smallmouth bass removed from 2001 through 2011; and (2) a capture-mark-recapture analysis of abundance, density, and exploitation of sub-adult and adult smallmouth bass from six reaches that provided sufficient data for the analysis from 2004 through 2011.

Methods

Study Species. Smallmouth bass is a popular and widely distributed piscivorous gamefish in North America. Their native range is from the Great Lakes, including the St. Lawrence River basin, to the southern fringes of the Ozark Mountains, and the Mississippi River to the western slope of the Appalachian Mountains (Wallus and Simon 2008). Smallmouth bass spawn at about 16ºC, and are most active (feeding) when water temperatures are 20–28°C. Smallmouth bass grow slowly at < 20ºC and are inactive in water below 10–15ºC (Webster 1954; Bennett and

Childers 1957; Coble 1967; Coutant 1975). Because of their preference for warm water, smallmouth bass prefer shoreline habitats in summer (Turner and MacCrimmon 1970; Coutant 1975; Wallus and Simon 2008). As water temperatures decline below 15ºC or approach their upper thermal avoidance threshold of 30ºC, smallmouth bass migrate to deeper water (Stroud 1948; Coutant 1975). Smallmouth bass are typically sedentary in summer, with net movement of < 0.62 miles but may migrate more than 47 miles to reach winter refugia (Wallus and Simon 2008). Smallmouth bass establish home ranges of several hundred meters (Etnier and Starnes 1993) and when displaced they display a strong homing instinct (Larimore 1952; Ridgway and Shuter 1996). Smallmouth bass prefer rock substrates as well as submerged woody debris (Miller 1975; Etnier and Starnes 1993). In streams, smallmouth bass show a preference for slack water and are not associated with strong currents (Coble 1975). As smallmouth bass grow their diet shifts from small crustaceans and other invertebrates to crayfish and fish with the switch to piscivory occurring at 15–70 mm, depending on the relative size of fish prey that are available (Reighard 1906; Hubbs and Bailey 1938; Coble 1975; Janssen 1992; Etnier and Starnes 1993; Boschung and Mayden 2004; Wallus and Simon 2008).

Study Area. Warm and cool water reaches of the upper Colorado River basin are included in the study area (Figure 1). While smallmouth bass have been captured, marked and removed from management units (reaches) throughout the upper Colorado River basin, data from only six reaches were sufficient to produce mark-recapture estimates of abundance (and density) and to calculate removal rates (e.g., exploitation) so those reaches will be the main focus of this analysis. One of these reaches included a section of the Colorado River and a small section of the Gunnison River, hereafter referred to as the Colorado-Gunnison (Table 1). The lower section of the Gunnison River was sampled as part of the effort to sample the Colorado River in all years (except 2003). Two of the six reaches included sections of the Green River: one reach referred to as the Middle Green, and another from Echo Park to Split Mountain, hereafter referred to as Echo-Split. The Yampa River had three reaches: most downstream Yampa Canyon; Lily Park; and most upstream Little Yampa Canyon.

Fish collection and removal. Electrofishing sampling and smallmouth bass removal was conducted by U.S. Fish and Wildlife Service (USFWS), Colorado Parks and Wildlife (CPW), Utah Division of Wildlife Resources (UDWR), and Colorado State University (CSU). Rafts were used in the Colorado-Gunnison, Echo-Split, and Yampa Canyon reaches and aluminum Jon boats were used in other reaches. Annual initiation and duration of sampling varied among reaches but were generally consistent within a reach; details (start date, end date, duration) for all reaches and years are provided as part of our descriptive results. Electrofishing consisted of pairs of concurrently operating electrofishing craft moving downstream, one boat on each shoreline. Electrofishing systems used 23 cm anode spheres hung from booms projecting 2 m in front of the bow and were half submerged. Rafts used one anode and Jon boats used two anodes spaced 1.5 m apart. On Jon boats, the boat hull was the cathode and on rafts the cathode was either broom-tail or fan-style cathode arrays suspended from each side. Electrofishing effort was recorded in seconds of pulsed direct current applied to the water by Coffelt VVP-15, Smith Root VVP-15B, or Smith-Root GPP 5.0, and ETS MBS (Verona, WI) electrofishing units.

Fish Processing & Tagging. After capture, bass were transferred to a live well and, depending on the reach, processed every 0.5–6 miles. Fish captured on one or more marking passes were measured to the nearest mm total length (TL), marked, and released. On non-marking (removal) passes, which represented the majority of sampling effort, marked and unmarked smallmouth bass were measured (TL) and removed from the river and either euthanized or translocated to off-channel reservoirs or Colorado State Wildlife Area ponds (Breton *et al.* 2013a).

The majority of the marks deployed were uniquely numbered, T-bar, model FD-94 anchor tags (Floy Tag and Manufacturing, Inc., Seattle, WA, U.S.A.) inserted between the pterygiophores of the dorsal fin using standard protocols (Guy *et al.* 1996). With only two exceptions, FD-94 anchor tags were deployed in five of the six reaches in all years. The two exceptions were the Colorado-Gunnison reach where bass were marked with caudal fin clips or punches in all years and the Middle Green reach in 2004 where bass were marked with non-numbered, T-bar, model FD-68B anchor tags (Floy Tag and Manufacturing, Inc.).

Life-Stage Allocation and Growth. We partitioned smallmouth bass into life stages based on their length: juveniles (<100 mm); sub-adults (100–199 mm); and adults (≥ 200 mm). In our descriptive summary of removals from all reaches, life-stage allocation was based on capture or recapture length just prior to removal. In our quantitative analyses of abundance in the six reaches we partitioned fish into adult or sub-adult life stages based on their predicted length on 1 May of the year of capture. Because water temperatures were relatively cool prior to about 1 June, our 1 May approach ensured that abundance reflected the population of sub-adult and adult fish available in a reach prior to onset of smallmouth bass growth that year. To estimate fish lengths on 1 May of each year, and also fish length on all electrofishing passes (more below), we used a two-step process. First we estimated the von Bertalanffy growth coefficient *k* and the asymptotic length L_∞ using the equation:

$$L_{i+1}^{g} = (g_{i+1} - g_i)k\left(L_\infty - L_i^{g}\right) + L_i^{g}$$

where L_i^g is the length on growth day *i* and g_i is the growth day; $g_{i+1} - g_i$_i is always equal to 1. In this growth analysis, we only used smallmouth bass that were marked, subsequently recaptured and had an initial capture and recapture length. A growth day was defined as any day when water temperatures were ≥ 20ºC, per the literature describing bass growth (Wallus and Simon 2008). The von Bertalanffy model was implemented recursively for each growth day between capture and recapture for each fish (see Breton *et al.* 2013b for more details).

The second step used the estimates of k and L_∞ (Appendix 1) to predict fish lengths on 1 May using the equation,

$$\widehat{L_{week\,\iota}} = (n)\hat{k}\left(\widehat{L_\infty} - L_i\right) + L_i$$

where L_i is the length at capture on the ith week and n is the number of days when water temperature was ≥ 20ºC between the capture date and seven days prior to this date. We back-calculated lengths in weekly steps backing up from initial capture or recapture date until we reached or went past 1 May. Estimates of k and L_∞ were also used to predict fish lengths on each pass using the equation,

$$\widehat{L_{Pass\,\iota}} = (n)\hat{k}\left(\widehat{L_\infty} - L_i\right) + L_i$$

where L_i is the length on pass i and n is the length n growth days before on pass i-1, or later on pass i+1. Fish length on each pass was used as an individual covariate in our mark-recapture analysis (see Breton *et al.* 2013b for more details).

Unless otherwise noted, water temperature data used for growth modeling were acquired from the nearest gauge downstream of the sampling reach (http://nwis.waterdata.usgs.gov/nwis, or http://www.fws.gov/mountain-prairie/riverdata/) for five reaches as follows: Colorado River (for fish caught upstream of the Gunnison River confluence, USGS Gauge #09095500; below, #09163500); Lower Gunnison River (#09152500 USGS Gauge); Middle Green (#09261000); Echo-Split (Mitten Park, USFWS); Yampa Canyon (#09260050); Lily Park and Little Yampa

Canyon (#09251000). For the sixth reach, Yampa Canyon, we used the Deerlodge Park gauge (#09260050) located just upstream.

Removal Summary & Data Analysis. We summarized the number of sub-adult and adult smallmouth bass removed each year by sub-basin for all reaches, 2001–2011. As noted above, allocation into the sub-adult or adult life stage was based on capture or recapture length just prior to removal in the sampling year. Also provided is the start of sampling each year, sampling duration in days, number of passes, non-native fish species that took priority in the electrofishing removal effort, sampling river start and river end miles.

For the six main sampling and removal reaches we used capture-mark-recapture (CMR) and removal data to estimate pre-removal and post-removal abundance of smallmouth bass using a Huggins closed population model (Huggins 1989, 1991; Williams *et al.* 2002; Bestgen *et al.* 2007a). From our estimates of abundance and reach lengths, we calculated reach densities before and after removal and exploitation rates for sub-adult and adult smallmouth bass. We used Program MARK to obtain abundance estimates as well as estimates of initial capture (p) and recapture (c) probabilities (White and Burnham 1999; White *et al.* 2001). We included several categorical variables (year, pass, life stage, behavior, year × pass, and year × behavior) to explain variation in our capture and recapture probabilities.

We included year effects because it was reasonable to assume that capture and recapture probabilities differed due to annual variation in environmental conditions such as flow, temperature, or differences in electrofishing crew efficiency. Similarly, we included electrofishing pass effects to account for capture probability variation which may have been affected by seasonal changes in discharge, conductivity, and water temperature. We included year × pass interactions to allow capture and recapture probabilities to be unique for each pass and year combination.

We also examined the potential that initial capture probabilities (*p*) might differ from recapture probabilities (*c*; White *et al.* 1982). For example, smallmouth bass might avoid electrofishing boats after their initial capture making $p > c$. To accommodate this effect we included a categorical variable referred to as 'behavior', that allowed initial capture probabilities to differ from recapture probabilities. We included the year × behavior interaction to allow the behavior effect to vary among years.

Capture probabilities of fish captured by electrofishing are typically a function of fish length (Snyder 2003 and references therein), where larger fish are usually more susceptible to capture than smaller ones. In our models, we initially used life stage (adult and sub-adult) to account for differences in *p* and *c* related to fish size. We subsequently replaced life stage in the best unconstrained model with the individual covariate, length (more below). To avoid confounding, length was not incorporated into models with life stage.

In each of our reach-specific abundance analyses, we started with an intercept-only model in which *p* and *c* were identical and constant. Then we attempted to fit all combinations of the effects described above, resulting in 27 models, including a model with the full set of effects and interactions. Parameter estimates from simpler models were used as starting values for more complex models to increase computational efficiency. Some complex models did not properly converge (produce reliable estimates), most likely due to sparse recapture data and/or effect sizes that were close to zero. Because nearly all sampling for each reach and year consisted of a single marking pass followed by multiple removal passes, it was not possible to assess goodness-of-fit of our capture-mark-recapture data using standard tests (Williams *et al.* 2002). In place of these tests, below we review assumptions of our closed population models and describe how we dealt with each case.

To meet the demographic closure assumption – no births, deaths, or recruitment within the study area during the sampling period – we allocated each fish, regardless of capture date, to a life stage based on its predicted length on 1 May thereby removing the possibility of recruitment from juvenile to sub-adult or sub-adult to adult life stages. Angling and natural mortality (death) of sub-adult and adult smallmouth bass were assumed minimal during the typically short (e.g., < 2 months) annual sampling seasons.

To assess the geographic closure assumption – no emigration or immigration relative to the study area during sampling – we combined all instances of marked smallmouth bass that were released and subsequently recaptured and categorized them as dispersers (recaptured in another reach) or residents (recaptured in the same reach as initial capture). Based on these data, dispersal within a sampling season was rarely observed: only 40 sub-adults out of 5,136 captures (0.8%) and 325 adults out of 7,093 captures (4.6%) moved out of its initial tagging reach in the season it was tagged. Although these within-season dispersal counts are probably low because of modest recapture rates in adjacent reaches, they demonstrate that movement rates were low and data met the geographic closure assumption.

To assess the CMR model assumption of minimal within-season Floy tag loss, several double-marking smallmouth bass studies were conducted in our study reaches. Of those, only the 2007 study in the Middle Green reach (*pers. comm.*, T. Hedrick, Utah Division of Wildlife Resources, Vernal) noted relatively low tag retention, where double-marked smallmouth bass (Floy tags and Passive Integrated Transponders) had 73% Floy tag retention over 120 days. The next year, tag retention by smallmouth bass in the Middle Green reach was 100% over a longer duration (186 days), suggesting tag application issues in 2007 were resolved. All other double-marking studies used fin clipping for the second mark and each of those also demonstrated high tag retention. For example, tag retention was 100% for smallmouth bass in Little Yampa Canyon after 19 days in 2007. In 2008, smallmouth bass tag retention was 96% for Echo-Split over 109 days, 96% for Yampa Canyon over 24 days, 100% for Lily Park over 77 days, and 100% for Little Yampa Canyon over 91 days. Thus, high tag retention estimates were presumed sufficient to avoid bias in the CMR abundance analyses.

Support for competing CMR models was quantified using Akaike weights (*w*; based on Akaike's Information Criterion for small sample sizes, AIC_c; Burnham and Anderson 2002). Akaike weights for competing models in a set sum to 1 and provide the relative degree of support for each model in the set. Model effects (logit scale) and estimates were considered statistically significant when the associated 95% confidence interval did not bound zero or bound the confidence interval of an adjacent estimate (Schenker and Gentleman 2001). We report log-transformed 95% confidence intervals (White *et al.* 2001) for our abundance estimates ($\widehat{N}$) with lower and upper boundaries $\hat{f}_0/_C + M_{t+1}$ and $\widehat{f_0} * C + M_{t+1}$, respectively, where $\widehat{f_0}$ is the number of animals never captured ($\widehat{N} - M_{t+1}$), M_{t+1} are the number of animals captured and,

$$C = \exp\{1.96 \times \sqrt{\ln[1 + \left(SE(\widehat{N})/_{\hat{f}_0}\right)^2]}\}.$$

To better understand effectiveness of removal efforts, we estimated annual exploitation rates for each of the six reaches, where exploitation rate was defined as the proportion of adult or sub-adult smallmouth bass removed. These rates were calculated as the number of fish removed by any method during or after sampling that year divided by the abundance estimate from that year. Density was estimated by dividing the pre-removal or post-removal abundance estimates by the reach length and is reported as fish per river mile. Pre-removal abundance is the estimate from the abundance analysis. Post-removal abundance was estimated as pre-removal abundance minus any fish removed during or after sampling.

<u>Long Term and Three-year Trends</u>. Sub-adult and adult pre-removal and post-removal density estimates from our abundance analyses (six reaches) were used to generate a summary table including trends. Using estimates from all years and just the last three years (2008-2010 for Colorado-Gunnison; 2009-2011 for the remaining five reaches), we determined long and short term trends (increasing, decreasing, or stable), respectively, for each reach and life stage. Given that electrofishing effort was generally (all six reaches) higher in the last three years relative to previous years the short term trends better reflect the status quo of the ongoing effort to control smallmouth bass proliferation and abundance in the upper Colorado River basin. As a result, we based all other summary data in our analysis of trends on just the last three years. We provide average pre-removal and post-removal densities from the last three years for all reaches and life stages. We calculated a percent bass recovery metric as the difference in post-removal density in year *i* from pre-removal density in year *i*+1 divided by pre-removal density in year *i*+1 multiplied by 100 and averaged over the last three years of available data. Percent recovery of smallmouth bass provides a relative estimate of recovery in a reach following electrofishing removal and other effects in the last three years. Exploitation from the last three years was also averaged to provide insight into efficiency of electrofishing removal. For three of our metrics, average pre-removal density, percent recovery and average exploitation, we also summarized the magnitude of estimates across reaches using a categorical scale: very low (VL); low (L); moderate (M); high (H); and very high (VH).

Consequence Table. To better understand effectiveness of smallmouth bass removal efforts, we developed a consequence table using abundance trends and density estimates from the six reaches included in our CMR abundance analyses. We specified one fundamental objective, to control numbers of sub-adult and adult smallmouth bass in six reaches in the upper Colorado River basin, and eight means objectives (Hammond *et al.* 1999). Means objectives are those that provide a 'means of achieving' the fundamental objective.

The first two means objectives are: minimize (1) sub-adult density and (2) adult density. These means objectives were used only for Echo-Split, Lily, and Little Yampa Canyon reaches. Colorado-Gunnison, Middle Green, and Yampa Canyon reaches were excluded because density estimates were not available in all years. The remaining six means objectives included all six reaches: maximize the proportion of the reaches that contain (3) ≤ 30 sub-adult bass per river mile and (4) ≤ 30 adult bass per river mile; maximize a declining trend for (5) sub-adult and (6) adult smallmouth bass; minimize rank based on the population estimate for (7) sub-adults and (8) adults. For means objectives 3 and 4, a value (score) was calculated for each year; for remaining objectives, a value (score) was calculated for each year and reach. For means objectives that refer to trends, a year was scored as 1 when the density of sub-adult or adult bass (depending on means objective) was higher in the previous year (declining trend) and a 0 otherwise. For rankings, each year received a rank in which a rank of 1 indicated lowest density in time-series and 8 indicated highest density in time-series. Objectives involving a 30 smallmouth bass/RMI density threshold were based on a Recovery Program interim goal that was developed for a 24-mile reach of habitat upstream of Yampa Canyon and later informally used as a criterion to measure smallmouth bass removal success in the Upper Basin as a whole (Chart *et al.* 2008; Tom Chart *pers. comm.*).

We envisioned the years 2004–2011 in our consequence table as representing alternative management outcomes, from electrofishing removal and environmental variation, and the purpose of the consequence table was to rank these outcomes. Among other insights, rankings allowed us to determine if control efforts in the basin have become more effective over time. Prior to plotting, scores for each alternative outcome (year) were normalized (Hammond *et al.* 1999). Normalization transforms all means objectives to the same 0–1 scale. Subsequently, the normalized scores were multiplied by 0.03 where 0.03 is the weight (same for all) that we allocated to each means sub-category of each means objectives (e.g., minimize adult density had 6 sub-categories representing each of the reaches included in the analysis). Across means objectives and sub-categories, weights summed to 1.0 in our analysis. Weighting is a way for analysts, if desired, to favor particular means objectives. These weighted scores were then summed across means objectives for each year and then plotted.

Results

Descriptive Summary

Counts of smallmouth bass removed by all gear types and sampling strategies are organized by sub-basin, reach, and year (2001–2011, Appendices 2-4). A total of 11,265 bass from all life stages (juvenile, sub-adult, adult, unknown) were removed from the Colorado-Gunnison reach from 2003–2011. A total of 48,840 bass were removed from the Green and White River sub-basins; the majority of these were removed from the Green River sub-basin (48,822). A total of 124,929 bass were removed from the Yampa River sub-basin.

Abundance Analyses

Model Selection

Colorado-Gunnison. Two models received all of the AIC_c weight (Table 2). Effects in the top model were year, pass and year × pass interactions for probabilities of capture. The second best model included these effects plus the behavior effect (0.2198 [–3.6228, 4.0624 95% CI]). The two models differed by 2 AIC_c units, evidence that the behavior effect did not improve model fit. The behavior effect was also very imprecise, 0.2198 (–3.6228, 4.0624 95% CI) so results from only the top model are interpreted. Models for this reach that included behavior × year interactions failed to converge.

Middle Green. The model including life stage, behavior, year, pass and year × pass interactions received 100% of the AIC_c weight so estimates from this model are presented below. Models including behavior × year interactions, and length failed to converge.

Echo-Split. The model containing length, year, pass and year × pass interactions received 95% of the AIC_c weight; estimates from only this model are presented. The second best model was identical to the top model except included the categorical variable life stage in place of the continuous covariate length. Models including behavior and behavior × year interactions failed to converge.

Yampa Canyon. The full set of 27 models, including those with interactions, properly converged in this analysis. The model including all main effects and interactions received 68% of the AIC_c weight and was used for estimation. The second best model excluded the behavior × year interactions (68 parameters) and received 32% of the model weight. Despite the penalty incurred in the AIC_c formula for having an additional seven parameters, the top model was still favored. Below we present estimates only from the top model.

Lily Park. The full set of 27 models, including those with interactions, properly converged in this analysis. The model containing all main effects and interactions received 100% of the AIC_c weight; estimates from this model are presented below.

Little Yampa Canyon. The full set of 27 models, including those with interactions, properly converged in this analysis. The model containing all main effects and interactions received 100% of the AIC_c weight; estimates from this model are presented below.

Estimates of Abundance, Density, and Exploitation

Colorado-Gunnison. Data necessary for our CMR abundance analysis were only available from 2006–2010 from this reach because smallmouth bass in 2004–2005 were removed, but never marked. There were too few adult smallmouth bass recaptures in 2011, and insufficient sub-adult recaptures in any year, to produce abundance estimates. Exclusion of sub-adults, with the resultant decrease in the length range of smallmouth bass used in this model, likely explains why length was not in top models in the Colorado-Gunnison abundance analysis. Electrofishing effort increased over time from 4-5 passes prior to 2007, to 9-10 passes from 2007 to 2011 (Table 3; number of passes in the Gunnison River section of this reach did not always match the number of passes in the Colorado River section, see Appendix 2 for more details).

Adult smallmouth bass density in the Colorado-Gunnison reach was relatively high in 2006 (close to 100 individuals per river mile prior to removal; Figure 2a) but then declined apparently due to natural mortality and emigration (Figure 2a). The 2006 density estimate was imprecise, typical of the first estimate in a time series, and resulted in a wide confidence interval that overlapped with confidence intervals for estimates in most other years. Following the apparent decline in 2007, density of adult smallmouth bass was relatively low and stable (fewer than about 20 individuals per river mile) through 2010. Density of smallmouth bass adults in the Colorado-Gunnison reach was never high relative to other locations (Figures 2–7), especially Lily Park (Figure 6b) and Little Yampa Canyon (Figure 7b) on the Yampa River.

Adult density after removal was only negligibly lower to that before removal in all years, indicating that exploitation was insufficient at reducing smallmouth bass density on an annual basis given rates of immigration and recruitment. Consistent with this observation, estimates of adult exploitation in the Colorado-Gunnison reach (10–31%; Figure 2b) were some of the lowest observed among the six reaches included in our abundance analyses. This occurred despite the substantial increase in passes and electrofishing hours after 2006 (Appendix 2).

<u>Middle Green</u>. Smallmouth bass were removed but not marked and released in this reach in 2005 and 2006. Hence, sufficient data were available only in 2004 and 2007–2011to produce CMR abundance estimates. In addition, the length of the Middle Green River removal reach varied among years. Our estimates apply only to a 71.4 mile-long sub-section of the reach that was consistently sampled (Split Mountain Boat Ramp [RM 319.3] to the Duchesne River Confluence [RM 247.9]). Electrofishing effort increased over time from 4 passes prior to 2007, to 9 passes in 2007 and 11–13 thereafter.

Pre-removal densities of sub-adult and adult smallmouth bass in the Middle Green River increased from 2004 to 2009 (Figure 3a-b) and then declined. Density estimates of each life stage in 2011 pre- and post-removal were the lowest in our 8-year time series. The Middle Green reach typically supported the lowest estimated densities of sub-adult (less than about 50 sub-adults per river mile) and adult (fewer than about 20 adults) smallmouth bass of all the reaches in our abundance analyses.

In most years,, sub-adult and adult smallmouth bass density estimates in the Middle Green River were substantially lower after removal. Unlike adult density estimates, confidence intervals associated with sub-adult pre- and post-removal density estimates typically overlapped. In spite of substantial reductions in smallmouth bass in some years due to removal, recruitment and immigration between the last removal sampling in one year and the first electrofishing pass in the next sometimes substantially increased smallmouth bass density in the reach. For example, after 2007 removal sampling was completed, recruitment and immigration increased sub-adult and adult smallmouth bass density by the time sampling began in 2008 to levels above both the pre- and post-density estimates from the prior year. The same scenario occurred from 2008–2009, in spite of a substantial removal effect in 2008.

Substantial removal of sub-adult and adult smallmouth bass in the Middle Green River reach in 2009 was not followed by a recovery of bass density through immigration and recruitment in 2010. Instead, post-removal sub-adult and adult densities from 2009 were further reduced, presumably because of natural mortality, emigration, and recruitment by sub-adults into the adult age class, when electrofishing resumed in spring 2010. Exploitation rates in the Middle Green River reach ranged from 40–60% for sub-adults and 50–80% for adults in most years for the period 2004–2011 (Figure 3c-d).

Echo-Split. Electrofishing effort increased over time from 4–5 passes prior to 2007 to 12–16 thereafter. Density of sub-adult and adult smallmouth bass was relatively high early in the study period but declined later (Figure 4a-b). An exception was the decline in the density of both life stages from 2004 to 2005, followed by subsequent recovery in 2006. A declining trend in density of sub-adult smallmouth bass was especially evident beginning in 2007; adult bass began to decline in 2006. Pre-removal sub-adult density estimates were the lowest for the 8-year time series in 2011, and adult smallmouth bass densities were the second lowest. Densities of sub-adult and adult smallmouth bass in the Echo-Split reach were higher (all years included in the abundance analysis) than those for the downstream Middle Green reach and the upstream Yampa Canyon reach.

Despite the precision of density estimates in most years, 95% confidence intervals associated with pre- and post-removal densities also often overlapped. However, increased removal effort beginning in 2007, coupled with reduced immigration rates due to increased effort in upstream and downstream reaches, and reduced recruitment within the reach is likely responsible for a steady decline in density of sub-adult and adult smallmouth bass in the reach. Exploitation of sub-adult and adult smallmouth bass was relatively low through 2006 but increased over time consistent with increased electrofishing removal effort (Figure 4c-d). Estimates of exploitation after 2006 were 25–50% for sub-adults and 35–60% for adult smallmouth bass.

Yampa Canyon. Smallmouth bass were removed but not marked and released in this reach in 2006 and 2007. Hence, sufficient data to produce CMR abundance estimates were available only for 2004–2005, and 2008–2011. A minimum of 4 and maximum of 8 electrofishing passes have been conducted in Yampa Canyon since 2001, where removal effort was (as elsewhere) constrained by flow conditions and river access.

Density of sub-adult smallmouth bass in Yampa Canyon declined over time beginning between 2005 and 2008, from nearly 150 individuals per mile in 2005 to < 10 per mile post-removal in 2011 (Figure 5a). Adult density estimates decreased sharply from 2004 to 2005 and, since that time, have remained relatively low and stable at about 10 adults per river mile pre- or post-removal (Figure 5b). Yampa Canyon smallmouth bass density was lower than the downstream Echo-Split reach, and substantially less than the upstream Lily Park reach.

Despite relatively precise density estimates in most years, 95% confidence intervals of pre- and post-removal sub-adult and adult estimates overlapped in most years (Figure 5a-b). Removal rates seemed relatively invariant to removal effort. For example, the highest electrofishing effort for the reach was implemented in 2009, but the adult density estimate in 2010 exceeded the pre-removal estimate from 2009 possibly due to recruitment of the remaining 2007 sub-adults into the adult age class. In spite of variable sampling effort over time, removal rates were apparently substantial enough to reduce and maintain relatively low sub-adult and adult smallmouth bass densities. This was doubtless aided by minimal immigration or recruitment; sub-adult smallmouth bass in Yampa Canyon increased substantially only once from 2004 to 2005, and similarly, adults increased only once from 2008 to 2009. Sub-adult exploitation was generally between 30 and 50% in the Yampa Canyon reach; exploitation estimates for adults approached 70% in two years, and were otherwise above 60% with the exception of 2005 and 2011.

Lily Park. After 2007, electrofishing effort more than doubled in this short reach from 26-40 hours to 71-97 hours per year when the number of passes increased from 4-6 to 7–9. Density patterns of sub-adult and adult smallmouth bass in this reach were variable over time (Figure 6a-b). Sub-adult smallmouth bass density increased from 2004–2006, declined dramatically in 2007, increased dramatically in 2008 and 2009, and declined thereafter despite (e.g.) the successful 2009 smallmouth bass cohort (Breton *et al.* 2013b). Adult smallmouth bass density was relatively high from 2004–2008, but declined after that. In general, Lily Park contained the highest densities of sub-adult and adult smallmouth bass of all reaches sampled.

The precision of Lily Park pre- and post-removal density estimates were high; the only exception was 2006 when few recaptures were available relative to other years. Relatively high and consistent removal rates were apparently offset by high rates of immigration and recruitment for both sub-adult and adult life stages (Figure 6c-d). High density of adults in Lily Park in 2008 was not expected because of low densities of sub-adult and adult life stages in 2007. High removal rates of sub-adults in 2008 and 2009 and reduced immigration and recruitment in 2010 and 2011 apparently resulted in reduced density of adult smallmouth bass in 2009–2011.

Exploitation rates for both sub-adult and adult smallmouth bass in Lily Park were the highest observed in the six reaches included in the study. Exploitation rates were relatively low for both life stages in 2006 and 2010, perhaps due to reduced sampling efficiency. Other than these years, exploitation was consistently above 65% and 75% for sub-adults and adults, respectively.

Little Yampa Canyon. From 2004–2007, annual electrofishing effort was about 200 hours; effort increased to about 300 hours from 2008–2010 and was over 400 hours in 2011. Consistent with increased effort, the number of sampling passes increased from a low of 7–9 from 2004 to 2008 to 10–14 thereafter.

Pre-removal density estimates of sub-adult smallmouth bass in the Little Yampa Canyon reach increased from 2004–2006, declined in 2007, increased and remained relatively stable from 2008–2010, and declined in 2011 (Figure 7a). The 2008–2010 increase in sub-adult bass was likely an artifact of a strong 2007 age-0 smallmouth bass cohort, and to a lesser extent the 2009 cohort (Breton *et al.* 2013b), which resulted in the highest pre-removal densities in the time series. Pre-removal density estimates of adult smallmouth bass in Little Yampa Canyon increased from 2004 to 2005, but then generally declined after that to the lowest density in our 8-

year time series in 2011 (Figure 7b). Pre-removal sub-adult densities of smallmouth bass in this reach were substantially lower than in the downstream Lily Park reach, while adult densities were higher.

Precision of pre- and post-removal density estimates for sub-adult and adult smallmouth bass in Little Yampa Canyon was high. Similar to the Lily Park reach, sub-adult immigration and recruitment rates exceeded removal rates in most years, which was responsible for increased density until 2010. Notably, the 2011 pre-removal sub-adult smallmouth bass density remained the same as the post-removal density from 2010 indicating little or no recruitment or immigration. Immigration and recruitment rates were also substantial for adult smallmouth bass in Little Yampa Canyon. The downward trend was enhanced by high removal rates of sub-adults over time and adult densities post-removal in 2011 were the lowest recorded during this study (Figure 7c).

Exploitation rates for both sub-adult and adult smallmouth bass in the Little Yampa Canyon reach were the second-highest observed in the six study reaches, and lower only than those for Lily Park. Exploitation rates were relatively low for both life stages in 2006 and 2010 (Figure 7c-d), perhaps due to reduced sampling efficiency. Other than those years, exploitation was consistently at or above 50% for sub-adults and 60% for adults.

Estimates of Capture and Recapture Probabilities

Estimates of capture (*p*) and recapture (*c*) probabilities from the top model (Table 2) from each of our abundance analyses are provided in Appendices 5-10. Comparisons of plots reveal substantial variation in capture and recapture probabilities across passes and among years and these patterns of variation vary across reaches. In those reaches that included an effect of length in top models (Table 2), such as Lily Park and Little Yampa Canyon (Appendices 9-10), the effect of fish length on detection (capture or recapture) was also substantial. Three fish lengths, 100, 200 and 300 mm, are plotted to demonstrate this effect. The negative effect of initial capture on recapture probability ("behavior effect") resulted in very low recapture probabilities relative to initial capture probability. Comparison of *p* and *c* plots in reaches including behavior in top models clearly demonstrates this effect, and Yampa Canyon is a good example of this (Appendix 8).

Long Term and Three-year Trends

Long term trends from the six reaches suggest declines in smallmouth bass abundance in 7 of 11 (64%) reach and life stage (sub-adult or adult) combinations and in 8 of 11 reach and life stage combinations (73%) over the short term (Table 4). Other long term trends for smallmouth bass were either increasing (one case), or stable (three cases). Other short-term trends were stable or decreasing. All short-term sub-adult trends were negative suggesting that despite the successful 2009 smallmouth bass cohort (Breton *et al.* 2013b) increased effort in recent years has had a negative effect on sub-adult smallmouth bass densities in all six reaches.

Based on our pre-removal density estimates, average sub-adult density in the last three years was anomalously high in Lily Park relative to the other reaches, 448 sub-adults/rmi versus 29-125 sub-adults/rmi, respectively. Middle Green had the lowest sub-adult density (low density) followed by Yampa Canyon (moderate density), Little Yampa Canyon (moderate density), Echo-Split (high density) and then Lily Park (very high density). Adult density was high in Lily Park and Little Yampa Canyon based on our point estimates, 66-69 adults/rmi versus 10-40 adults/rmi for all other reaches. The lowest densities of adults were encountered in the Middle Green and

Yampa Canyon reaches (low density) followed by Echo-Split and Colorado-Gunnison (medium density), Little Yampa Canyon and then Lily Park (high density).

Percent smallmouth bass recovery in the last three years for sub-adults was negative (fewer sub-adults in the spring relative to the fall) in Echo-Split and Yampa Canyon. All other reaches showed some sub-adult recovery, ranging from 6% in Middle Green and Lily Park reaches (low recovery) to 38% in Little Yampa Canyon (high recovery). Despite smallmouth bass percent recovery trends, sub-adult exploitation was lowest in Echo-Split and Yampa Canyon (0.28–0.38) followed by Middle Green and Little Yampa Canyon (0.49–0.52) and highest in Lily Park (0.63). Percent recovery for adult bass was positive in all reaches. Middle Green and Echo-Split showed low adult recovery (34-35%) followed by Colorado-Gunnison (moderate; 78%), Little Yampa Canyon (high, 178%), Lily Park (high, 208%) and Yampa Canyon (high, 214%). Adult exploitation by electrofishing removal was very low in the Colorado-Gunnison reach; moderate in Echo-Split and Yampa Canyon and relatively high in all other reaches.

Additional Removal Reaches

Several other reaches in the upper Colorado River basin were sampled and smallmouth bass were removed from 2001–2011 (Appendices 2-4), but data were insufficient to perform CMR analyses based on an evaluation of available data performed by the lead author in 2010. In the Green River sub-basin, additional removal reaches included Desolation Canyon, Lodore Canyon, and the White River (Appendix 3). Removal sampling is ongoing in the latter two reaches and intermittent in Desolation Canyon as bass populations fluctuate. Additional reaches of the Yampa River were also sampled beginning in 2005 or after to provide more comprehensive removal efforts, and included Cross Mountain, Sunbeam, Lower and Upper Maybell, Juniper, South Beach, and Hayden to Craig (Appendix 4). Substantial removal of smallmouth bass occurred in some of those areas including Upper Maybell, Juniper, and South Beach. Recent expansion of smallmouth bass populations in locations such as the White River and ongoing removal efforts in others suggest future analyses of that data may be merited if sufficient data are available.

Consequence Table

Weighted scores from our consequence table indicated an increase in smallmouth bass control effectiveness via electrofishing removal and an overall decline in smallmouth bass abundance and density for sub-adults and adults in the upper Colorado River basin from 2004–2011 (Figure 8). The decline in removal effectiveness in 2008 and 2009 was likely caused by the high growth, survival, and recruitment success of age-0 smallmouth bass produced in 2007 throughout the upper Colorado River basin. Since 2008, weighted scores increased steadily and years 2010 and 2011 exceeded all others in the study period, suggesting smallmouth bass control has been increasingly effective. .

Discussion

The rapid increase in smallmouth bass density in warm-water streams of the upper Colorado River basin has resulted in reductions in native species and initiated intensive smallmouth bass removal efforts (Haines and Modde 2007; Hawkins *et al.* 2009). We describe current trends in density of smallmouth bass and provide potential explanations for those patterns. In general, three factors explain patterns in abundance fluctuations: reductions due to effects of removal via electrofishing; smallmouth bass recovery after exploitation due to recruitment or immigration;

and changes due to environmental factors not related to electrofishing and other management actions.

Removal and density dynamics. Removal efforts in the upper Colorado River basin have generally resulted in declining trends in smallmouth bass abundance in all reaches that were sustained through 2011 under environmental conditions that were prevalent during this time. The lack of bass recovery from 2010 to 2011 was particularly notable in Little Yampa Canyon, a reach that typically recovered quickly from removal efforts in prior years. The consequence table also supported the notion that the accumulated effects of mechanical removal were successful in reducing smallmouth bass abundance. However, analyses also indicated that years with high smallmouth bass reproduction (e.g., 2007) and recruitment (e.g., 2008, 2009) can cause substantial increases in density in the following years, negating removal efforts.

The effects of electrofishing removal of smallmouth bass can be seen most clearly in the Middle Green, Lily Park and Little Yampa Canyon reaches. In almost every year, particularly after 2007, adult post-removal density was lower than the pre-removal estimate, indicating a significant within-year reduction in adult smallmouth bass density due to electrofishing removal. Significant removal of sub-adults was also achieved but with less consistency. Exploitation rates in Lily Park and Little Yampa Canyon were consistently high for adult and sub-adult smallmouth bass, exceeding 80% in many years. These levels of exploitation may be necessary to obtain long-term reductions in density.

A similar pattern of reduced within-year density due to removal can be seen in some years in the Echo-Split and Yampa Canyon reaches. However, overall densities in these reaches are much lower than in Lily Park or Little Yampa Canyon and the effect of removal is less pronounced. Exploitation in these reaches was also high, exceeding 60% in most years where a significant density reduction was accomplished. The Colorado-Gunnison reach showed very little within-year density reduction due to removal efforts and had the lowest observed exploitation rates.

After 2008, smallmouth bass population recovery in Echo-Split and Lily Park reaches was less pronounced than previous years and adult densities declined. Electrofishing removal effort in Echo-Split was increased substantially in 2007 to increase exploitation (Haines and Modde 2007) and subsequently adults declined. A similar decline in adults occurred in Lily Park after electrofishing effort was increased in 2008 from 6 to 8 or 9 passes. These trends provide evidence that intensive removal efforts (ca. since 2007) have led to a substantial reduction in numbers of adult bass and demonstrate that intensive exploitation can minimize and possibly overcome the counter-effects of immigration and recruitment. Reductions observed in specific reaches may also be due to removal efforts in upstream and downstream reaches. For example, the declining trend in adult density in the Middle Green reach may be due, in part, to intensive removal efforts in the upstream reach, Echo-Split, since 2007. Similarly, low densities of adults in Yampa Canyon over most of the years may be the result of intensive removal there and in upstream Lily Park.

Despite significant reductions due to electrofishing removal in some reaches, density of smallmouth bass tended to recover the following year. Recovery of smallmouth bass abundance was especially evident in Lily Park and Little Yampa Canyon. The recovery of smallmouth bass density in such reaches was due either to immigration from other areas, reproduction and recruitment within the reach, or both. Reproduction within the river system has been well documented and probably occurs throughout the upper Colorado River basin (Bestgen *et al.* 2007b; Hawkins *et al.* 2009). Some reaches, such as Little Yampa Canyon, are thought to be especially ideal habitats for smallmouth bass reproduction because of availability of low velocity and rocky shoreline habitat, which likely resulted in a source of recruits for that reach and others downstream. For instance, we speculate that fish produced in Little Yampa Canyon may be a driver for population dynamics trends seen in downstream reaches such as Lily Park. The mechanism may be production and dispersal of abundant juvenile or sub-adult smallmouth bass from Little Yampa Canyon downstream during high runoff in spring or a general downstream dispersal pattern as has been shown by this species in other parts of its range (Humston *et al.* 2009).

Upper Colorado River basin reservoirs, such as Elkhead Reservoir, are a significant source of smallmouth bass in the Yampa River (Breton *et al.* 2013a). For example, smallmouth bass escapement rates from Elkhead Reservoir into Elkhead Creek, a tributary of the Yampa River, ranged from 35 to 64% for cohorts of smallmouth bass stocked into Elkhead Reservoir from 2003–2005 and were as high as 23% after that time. Escapement rates were almost certainly underestimates of actual escapement from that single off-channel source (see Breton *et al.* 2013a for details). Ultimately, reproduction and subsequent immigration to other reaches are probably linked, and both play a role in observed population increases after removal (Hawkins *et al.* 2009). Defining movement of various life stages of smallmouth bass would allow a more complete understanding of population dynamics and allow targeting of removal in production reaches that may be supplying recruits to adjacent reaches.

Reduced density of smallmouth bass due to electrofishing removal may also enhance population recovery (Zipkin *et al.* 2008; 2009). Smallmouth bass have a documented compensatory response to exploitation where removal of adults increases abundance of young (Weidel *et al.* 2007; Zipkin *et al.* 2008, 2009) or recruitment to adult stock size (Peterson and

Kwak 1999). For example, following a smallmouth bass removal effort undertaken to enhance native fishes (Weidel *et al.* 2007; Zipkin *et al.* 2008), smallmouth bass biomass declined, (Weidel *et al.* 2007) but smallmouth bass abundance increased due to recruitment of smaller immature individuals (Zipkin *et al.* 2008). Demographic modeling also suggested that exploitation may increase abundance in species like smallmouth bass (Zipkin *et al.* 2009). We have little direct evidence other than the "saw toothed" pattern in many of our reach-specific density plots that density-dependent compensatory mechanisms are responsible for population trends observed in the upper Colorado River basin. However, since density-dependent mechanisms have been demonstrated in other smallmouth bass populations, we suggest that density-dependent compensation be explored in greater detail in the future; those efforts should be guided by the population model under development (*unpubl. data*, Report Authors).

Environmental Factors. Our results also illustrate that environmental factors were responsible for dramatic fluctuations in smallmouth bass densities in the upper Colorado River basin. For instance, high, late, and cool flows such as those observed in 2005, 2008, and 2011 resulted in later spawning and reduced length and abundance of age-0 smallmouth in autumn in the Yampa and middle Green River systems (*unpubl. data*, KRB). The declines in sub-adult abundance seen in Echo-Split and Lily Park reaches in the years following these high flow events (2006, 2009, 2012, unpublished data) may be due to decreased reproduction and recruitment the previous year. The opposite environmental conditions were observed in, e.g., 2006 and 2007 when smallmouth bass reproduction was early in the year and growth rates and recruitment of young smallmouth bass was high. Increased sub-adult smallmouth bass abundance observed in many reaches in 2008 and 2009 (e.g., Middle Green, Lily Park, Little Yampa Canyon) was probably related to positive recruitment conditions in 2006 or 2007. Colorado-Gunnison and Yampa

Canyon reaches also showed similar patterns of declines that cannot be attributed to removal but instead may be due to environmental effects.

Assumptions Affecting Abundance Estimates. It is well established in the closed population, capture-mark-recapture literature that heterogeneity in capture and recapture probabilities will result in an underestimate of abundance (Seber 1982; Borchers *et al.* 2002). Heterogeneity can arise when the easiest to capture individuals are captured first and harder to capture individuals remain, a common phenomenon in mark-recapture studies. To avoid underestimating abundance, we included covariates that accounted for some of the heterogeneity in our data, including pass, year, fish length, behavior, and interactions among these factors. However, some unexplained heterogeneity may remain and we recommend that abundance estimates and densities be interpreted as minima. We also recommend caution interpreting estimates of exploitation rates, because those are explicitly linked to abundance estimates.

Violation of the geographic closure assumption was possible in our study because reaches were not blocked to eliminate movement of bass into or out of reaches. However, estimates of within-season dispersal based on tag recaptures suggested only 1% of sub-adults and 5% of adults dispersed from reaches in the season they were marked. Given these low dispersal rates, we believe that our estimates of abundance were minimally affected. Reduced tag retention in smallmouth bass has been demonstrated and may have also biased our abundance estimates (Walsh and Winkelman 2004). However, tag loss studies conducted on smallmouth bass in the upper Colorado River basin suggested, with one minor exception, retention was 96–100% over 19–186 days. Additionally, other studies have reported high retention rates of FD-94 anchor tags over the sampling intervals we used (Buzby and Deegan 1999; Gurtin *et al.* 1999; Livings *et al.*

2007). Based on the relatively short sampling duration when tag loss was relevant, we feel confident that density estimates were not unduly biased.

Benefits of Tagging Fish. Marking and releasing smallmouth bass on one or more passes to provide the data necessary to perform mark-recapture analyses has not always been part of the protocol encouraged by the Recovery Program (Hawkins *et al.* 2009). A removal-only strategy for controlling smallmouth bass in the upper basin was prevalent in prior years. This alternative is often brought-up in discussions, such as those arising at Recovery Program Non-native Fish Workshops held annually in December. In this section, we review well known problems with count data and then follow with some benefits of marking fish for the present study.

Counts of fish removed, such as those presented in our descriptive analysis, are a function of not just the abundance of fish in the area sampled but also a suite of effects including environmental (e.g., flow, temperature, turbidity) and effects associated with sampling gear (e.g., electrofishing unit, crew experience). The influence that these effects have on counts can be substantial, such as the effects of pass, year and their interaction presented in this report (Appendices 5-10). The effect of fish length and behavior on capture and recapture efficiency were also substantial in many reaches. These effects demonstrate the unreliability of count data for use in evaluation of the effectiveness of removal efforts. The unreliability of count data in general is well known. In fact, an entire sub-discipline in quantitative ecology has evolved in the last ca. 40 years to develop and investigate capture-mark-recapture models that correct counts for imperfect detection in wildlife and fisheries studies (Williams *et al.* 2002). A popular fisheries metric, catch-per-unit-effort (CPUE), a ratio of a count and associated effort, is not immune to imperfect detection.

Despite the investment required to capture, mark and subsequently recapture marked fish, the benefits of marking and releasing fish, rather than just removing them on initial capture, are many. In general, the only reliable conclusion we can draw from our descriptive analysis is that 185,034 smallmouth bass were removed from the upper Colorado River basin from 2001-2011. Because of the reality of imperfect detection, the counts presented in Appendices 2-4 cannot be used to make reliable inferences to the sampled population including abundance, density, and length-frequency distributions, nor to total removal levels. In contrast, for the six reaches that provided sufficient data, mark-recapture models were used to correct counts of fish detected in six reaches and estimate population abundances. These abundance estimates were then used to estimate density, a metric that makes sense for comparing study areas of varying size such as river reaches. We were also able to split density into pre- and post-removal components and make inferences regarding the contribution of electrofishing removal, recruitment, natural mortality, immigration, emigration and environmental effects to population dynamics of smallmouth bass in our six primary study reaches. These insights have since been integrated into a comprehensive smallmouth bass population dynamics model which is being used to formulate control strategies and other management recommendations (*unpubl. data*, Report Authors). Mark-recapture data from Little Yampa Canyon were used to demonstrate how length-frequency distributions can be corrected for imperfect detection (Breton *et al.* 2013b). In addition, all of the mark-recapture data from the six reaches were necessary for the analysis of smallmouth bass escapement from Elkhead Reservoir performed by Breton *et al.* (2013a).

Keeping in mind that counts are little more than total fish removed in the absence of mark-recapture data and the many benefits mark-recapture data provide (our list above is not exhaustive), we recommend that the decision to switch to removal-only, or an alternating scenario whereby removal-only is conducted exclusively in some years (e.g., every other), for smallmouth bass in a reach should be done only after careful discussion. These discussions should include consideration of one or more potential criteria for determining when a reach should switch from mark-recapture to removal only. One possible criterion, to assist with a decision to switch to a removal-only or an alternating strategy, is the ability to estimate abundance with reasonable precision where 'precision' might be quantified as a coefficient of variation (CV): $(\widehat{SE}(\widehat{N})/\widehat{N}$ where $\widehat{N}$ is an estimate of abundance and $\widehat{SE}(\widehat{N})$ is its estimated standard error. Managers should consider using multiple criteria, and these criteria may vary among reaches. It should also be kept in mind that an imprecise abundance estimate one year may not translate into an imprecise estimate the following year. Reasons for a poor estimate include environmental variation that affects recapture rates. Imprecise estimates should be discussed, and application of criteria for discontinuing mark-recapture should only be made after careful discussion.

Summary. Our analyses indicated smallmouth bass densities were substantially reduced by annual electrofishing removal efforts in affected reaches in the upper Colorado River basin under environmental conditions prevalent during the study. In addition, increased electrofishing removal efforts since about 2007 may have resulted in sustained reductions in smallmouth bass density. We recommend that removal efforts continue at an intensity and distribution in the upper Colorado River basin similar to 2011 but that managers consider reallocating effort based on population trends and removal success. For instance, reproduction, recruitment, and movement of smallmouth bass may have allowed densities to recover in some reaches, particularly portions of the Yampa River. Recovery of smallmouth bass in such areas implied that nearby reaches were important for age-0 production (e.g., upstream South Beach reach, Little Yampa Canyon) to sustain populations where high removal occurred (e.g., Lily Park, Little Yampa Canyon). Specifically targeting removal of all life stages of smallmouth bass in such production reaches (e.g. South Beach expanded late spring and early summer removal to target spawning adults and early young-of-year) may result in reductions in downstream populations that rely on upstream sources for recruitment. We recommend continued assessment of smallmouth bass populations in reaches where high reproduction occurred, such as Little Yampa Canyon. It may be necessary to expand monitoring to areas surrounding suspected sources of smallmouth bass and increase removal effort in these reaches. Such an effort was initiated in 2010 by the Recovery Program and is now colloquially referred to as “the surge”. Removal effort that, historically, , produced very lower removal rates such as early spring electrofishing passes conducted in Little Yampa Canyon, should be considered for reallocation to overlap with (time and space) smallmouth bass production areas. Reallocation of existing effort will increase removal rates, reduce recruitment, and minimize the need to find additional resources for increasing electrofishing effort in the basin.

The ability of smallmouth bass to produce large year classes and successfully recruit juveniles to sub-adult and adult life stages, combined with the high cost and potentially temporary effects of mechanically removing smallmouth bass from these large rivers, also suggested a need to examine alternative means of control for this invasive species (see related challenges and discussion in Coggins *et al.* 2011 and Loppnow *et al.* 2013). Reducing or eliminating escapement from upstream reservoir populations (e.g., Elkhead Reservoir) will reduce abundance of all life stages in downstream reaches (Breton *et al.* 2013a). In dam-controlled reaches such as the Green River downstream of Flaming Gorge Reservoir, short-term flow releases that are higher or cooler than ambient conditions may reduce reproductive success of smallmouth bass. Alternatively, stream flows altered via diversions or climate change may also be an important factor influencing smallmouth bass population abundance. This is because alterations to timing of peak flows and reductions in peak and base flows may result in earlier spawning and increased growth and survival of early life stages of smallmouth bass, and cascading increases in sub-adult and adult life stages. Effects of such alternative scenarios and means of control can be explored with a simulation modeling tool (*unpubl. data*, Report Authors).

Conclusions

1. Electrofishing removal of smallmouth bass in the upper Colorado River basin has been effective under environmental conditions prevalent during sampling to reduce abundance of sub-adult and adult smallmouth bass from selected reaches.
2. Environmental factors also contributed to substantial declines and increases (through conditions conducive to high recruitment in some years) in smallmouth bass abundance.
3. Substantial recruitment of year classes produced in low flow and warm years can offset removal efforts.
4. Immigration from production areas to other parts of the upper basin, e.g., Little Yampa Canyon to downstream reaches, may be responsible for increased abundance of sub-adults but mechanisms for those dynamics are poorly understood.
5. The intensity and distribution of electrofishing effort by the Recovery Program and its collaborators from about 2007 to 2011 does not appear to be sufficient, by itself, for reducing smallmouth bass population size in the upper Colorado River basin, as a whole, or any of its sub-basins, below the threshold necessary to cause recruitment failure.

6. Use of tagged fish was essential to understand abundance dynamics of smallmouth bass in the upper Colorado River basin.

Recommendations

1. Continue removal of smallmouth bass from reaches of the upper Colorado River basin at an intensity and distribution similar to effort expended in 2011.
2. Reallocate removal effort that historically produced very low removal rates (e.g., early spring sampling in Little Yampa Canyon) to areas perceived to be production areas to increase adult smallmouth bass removal rates and decrease productivity (recruitment).
3. If additional electrofishing resources (time, funding, and crews) become available, then consider allocating these resources to removal in areas perceived to be production areas to increase adult smallmouth bass removal rates and decrease productivity (recruitment).
4. Consider other tools such as flow or temperature fluctuations to reduce smallmouth bass reproductive success in production areas. This recommendation applies in particular to the Green River upstream and downstream of the Yampa River.
5. Maintain the management strategy to not translocate smallmouth bass to Elkhead Reservoir and other locations in the upper Colorado River basin.
6. Prevent escapement of resident smallmouth bass and other fishes from Elkhead Reservoir and other sources into streams of the upper Colorado River basin.
7. Continue use of tagged fish to obtain reliable abundance estimates to understand dynamics of smallmouth bass in the upper Colorado River basin.
8. Analyze capture-recapture data on a schedule determined appropriate by basin managers to evaluate effectiveness of ongoing removal efforts, including reaches not integrated into the

CMR portion of this report, which may now have sufficient data to conduct a more in-depth analysis.

9. Evaluate switching to removal of smallmouth bass on all passes (no tagging), or an alternating removal in some years and removal with mark-recapture in others, in reaches only when pre-determined criteria are met. A reduction in number of recaptured fish below that needed to obtain a reliable abundance estimate may be one such criterion.
10. Integrate re-evaluations of effectiveness of smallmouth bass removal efforts into a carefully designed adaptive management strategy to assess implications for recovery of the four endangered fish species.

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Table 1. River mile start and end locations and the extent of the six focal reaches included in the capture-mark-recapture abundance analysis. The Colorado and Gunnison reaches were combined into a single reach.

Reach	Location (river miles)	Extent of removal (miles)
Colorado & Gunnison Rivers		
Colorado	152.6–185.6	33
Gunnison	0–2.3	2.3
Green River		
Middle Green	247.9–319.3	71.4
Echo Park-Split Mt.	319.6–345.6	26
Yampa River		
Yampa Canyon	0–46	46
Lily Park	50.5–55.5	5
Little Yampa Canyon	100–124	24

Table 2. Capture-recapture models by river reach and model selection criteria including Akaike's Information Criterion adjusted for small sample size (AIC_c), Δ AIC_c and AIC_c weights for top models from the abundance estimation analyses in each of six river reaches in the upper Colorado River basin (see results for details on river reaches and model effects). Also provided are the number of parameters in the model (#P) and model deviance.

Reach	**Model**	**AIC_c**	**Δ AIC_c**	**AIC_c Weight**	**#P**	**Deviance**
Colorado-Gunnison	year+pass+year*pass	4255.65	0.00	0.73	29	4197.29
	behavior+year+pass+year*pass	4257.67	2.02	0.27	30	4197.28
Middle Green	stage+behavior+year+pass+year*pass	43477.94	0.00	1.00	55	43367.83
Echo-Split	length+year+pass+year*pass	45403.22	0.00	0.95	85	45233.00
	stage+year+pass+year*pass	45409.25	6.03	0.05	85	45239.02
Yampa Canyon	length+behavior+year+pass+year*behavior+year*pass	34545.33	0.00	0.68	38	34469.26
	length+behavior+year+pass+year*pass	34546.85	1.52	0.32	33	34480.80
Lily Park	length+behavior+year+pass+year*behavior+year*pass	63533.79	0.00	1.00	64	63405.70
Little Yampa Canyon	length+behavior+year+pass+year*behavior+year*pass	64372.82	0.00	1.00	75	64222.70

Table 3. Annual summary of boat-based electrofishing effort from the six reaches in the upper Colorado River basin included in our abundance analyses for smallmouth bass (*Micropterus dolomieu*). Start, end and days describe the electrofishing sampling period each year (Yr). Electrofishing effort (Elect. Effort) gives the number of electrofishing passes (#p) and number of electrofishing hours in parentheses. Additional details are provided in Appendices 2-4.

River	**Reach**	**Yr**	**Start (m/d)**	**End (m/d)**	**Days**	**Elect. Effort #p (hrs)**	**River**	**Reach**	**Yr**	**Start (m/d)**	**End (m/d)**	**Days**	**Elect. Effort #p (hrs)**
CO	Colorado River	2004	7/6	8/28	54	4 (182)	YA	Yampa Canyon	2004	4/14	7/22	100	8 (122)
CO	Colorado River	2005	7/12	8/25	45	4 (202)	YA	Yampa Canyon	2005	6/13	7/29	47	5 (172)
CO	Colorado River	2006	7/5	9/19	77	5 (208)	YA	Yampa Canyon	2006	6/5	9/28	116	6 (179)
CO	Colorado River	2007	6/20	10/3	106	9 (411)	YA	Yampa Canyon	2007	6/5	6/28	24	4 (112)
CO	Colorado River	2008	7/7	10/17	103	9 (420)	YA	Yampa Canyon	2008	7/8	8/1	25	4 (155)
CO	Colorado River	2009	6/30	9/30	93	9 (454)	YA	Yampa Canyon	2009	4/7	7/17	102	7 (200)
CO	Colorado River	2010	7/7	9/29	85	9 (467)	YA	Yampa Canyon	2010	6/1	7/16	46	6 (179)
CO	Colorado River	2011	8/9	10/26	79	10 (510)	YA	Yampa Canyon	2011	7/5	8/12	39	6 (183)
GU	Gunnison River	2004	7/9	8/17	40	4 (12)	YA	Lily Park	2004	4/24	7/7	75	6 (26)
GU	Gunnison River	2005	7/27	8/26	31	4 (12)	YA	Lily Park	2005	5/4	7/19	77	6 (35)
GU	Gunnison River	2006	7/26	9/12	49	5 (11)	YA	Lily Park	2006	4/25	6/20	57	6 (37)
GU	Gunnison River	2007	7/20	9/28	71	9 (27)	YA	Lily Park	2007	4/17	7/29	104	6 (40)
GU	Gunnison River	2008	8/6	10/14	70	7 (?)	YA	Lily Park	2008	4/22	7/8	78	9 (83)
GU	Gunnison River	2009	7/29	9/17	51	9 (28)	YA	Lily Park	2009	4/28	7/7	71	8 (97)
GU	Gunnison River	2010	7/28	9/24	59	9 (31)	YA	Lily Park	2010	4/13	6/27	76	8 (71)
GU	Gunnison River	2011	8/11	10/20	71	9 (37)	YA	Lily Park	2011	5/10	8/7	90	7 (71)
GR	Middle Green	2004	4/30	8/26	119	4 (173)	YA	Little Yampa Canyon	2004	4/22	7/8	78	9 (195)
GR	Middle Green	2005	3/21	9/27	191	4 (163)	YA	Little Yampa Canyon	2005	4/22	7/21	91	9 (220)
GR	Middle Green	2006	3/27	10/26	214	4 (221)	YA	Little Yampa Canyon	2006	4/20	7/14	86	7 (211)
GR	Middle Green	2007	3/27	10/30	218	9 (261)	YA	Little Yampa Canyon	2007	4/18	9/9	145	8 (193)
GR	Middle Green	2008	3/26	10/24	213	12 (546)	YA	Little Yampa Canyon	2008	4/15	9/7	146	7 (295)
GR	Middle Green	2009	3/25	10/15	205	13 (470)	YA	Little Yampa Canyon	2009	4/7	9/19	166	11 (301)
GR	Middle Green	2010	4/8	10/21	197	11 (476)	YA	Little Yampa Canyon	2010	4/15	9/18	157	10 (284)
GR	Middle Green	2011	3/23	10/12	204	11 (553)	YA	Little Yampa Canyon	2011	4/26	8/21	118	14 (407)

GR	Echo-Split	2004	8/3	9/16	45	4 (112)
GR	Echo-Split	2005	8/2	8/30	29	4 (84)
GR	Echo-Split	2006	7/18	9/7	52	5 (84)
GR	Echo-Split	2007	7/2	9/26	87	15 (323)
GR	Echo-Split	2008	6/16	10/3	110	16 (324)
GR	Echo-Split	2009	6/20	9/28	101	16 (288)
GR	Echo-Split	2010	6/21	10/7	109	15 (307)
GR	Echo-Split	2011	7/19	9/30	74	12 (215)

Table 4. Smallmouth bass (*Micropterus dolomieu*) long and short term trends (increasing, decreasing, or stable) for each reach and life stage for reaches included in our abundance estimation analyses in the upper Colorado River basin. Electrofishing effort was generally (all six reaches) much higher in the last three years relative to previous years so the short term trends better reflect the recent status of the ongoing effort to reduce smallmouth bass abundance. Thus, most columns in the table were based on only the last three years of sampling information (2009-2011 for all reaches except the Colorado-Gunnison, which was 2008-2010). Average pre- (PreR) and post-removal (PostR) densities from the last three years for all reaches and life stages were calculated. Percent recovery is the difference in post-removal density in year *i* from pre-removal density in year *i*+1 divided by pre-removal density in year *i*+1 multiplied by 100 and averaged over the last three years. Exploitation is the annual % of fish removed from a reach and is an average from the last three years. Three of our metrics, average pre-removal density, % recovery and average exploitation, were summarized across reaches using a categorical scale: very low (VL); low (L); moderate (M); high (H); and very high (VH).

River	**Reach**	**Stage**	**Trend (all years)**	**Trend (3 yrs)**	**PreR Density (3 yrs)**	**PreR Category (3 yrs)**	**PostR Density (3 yrs)**	**% Recovery (3 yrs)**	**%Recov. Category (3 yrs)**	**Exploit. Rate (3 yrs)**	**Exploit. Category (3 yrs)**
CO, GU	Colorado-Gunnison	Subadults	estimates not available								
		Adults	↓	→	36	M	30	78	M	0.20	VL
GR	Middle Green	Subadults	→	↓	29	L	15	6	M	0.49	M
		Adults	→	↓	10	L	4	35	L	0.65	H
GR	Echo-Split	Subadults	↓	↓	125	H	94	-5	L	0.28	L
		Adults	↓	↓	40	M	29	34	L	0.32	M
YA	Yampa Canyon	Subadults	↓	↓	69	M	42	-42	L	0.38	L
		Adults	↓	→	14	L	6	214	H	0.54	M
YA	Lily Park	Subadults	→	↓	448	VH	185	6	M	0.63	H
		Adults	↓	→	69	H	20	208	H	0.79	H
YA	Little Yampa Canyon	Subadults	↑	↓	80	M	41	38	H	0.52	M
		Adults	↓	↓	66	H	25	178	H	0.66	H

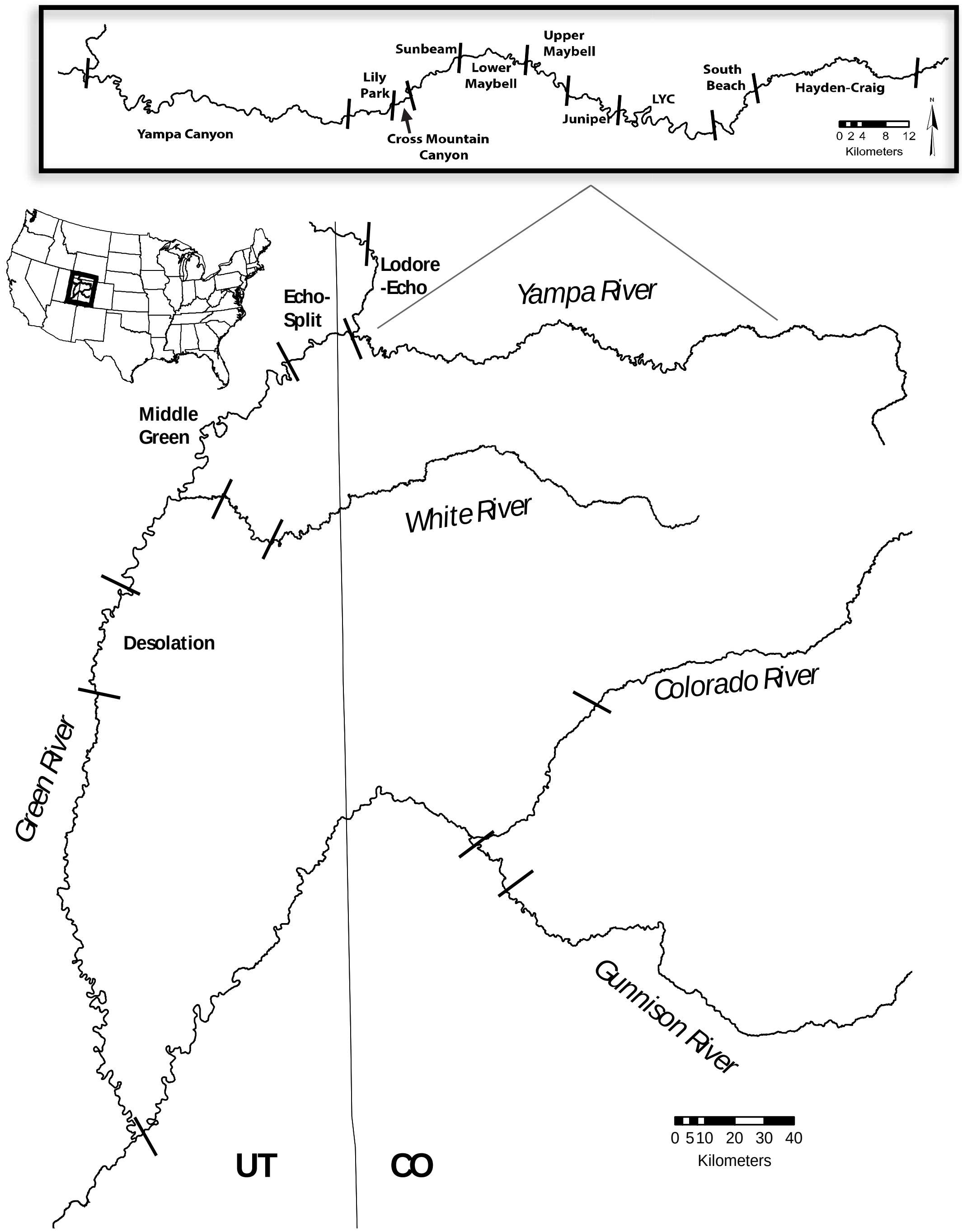


Figure 1. The Green and Colorado River drainages and sampling reaches of the upper Colorado River basin. Sampling reaches and river miles discussed in text are demarcated by bars perpendicular to the river.

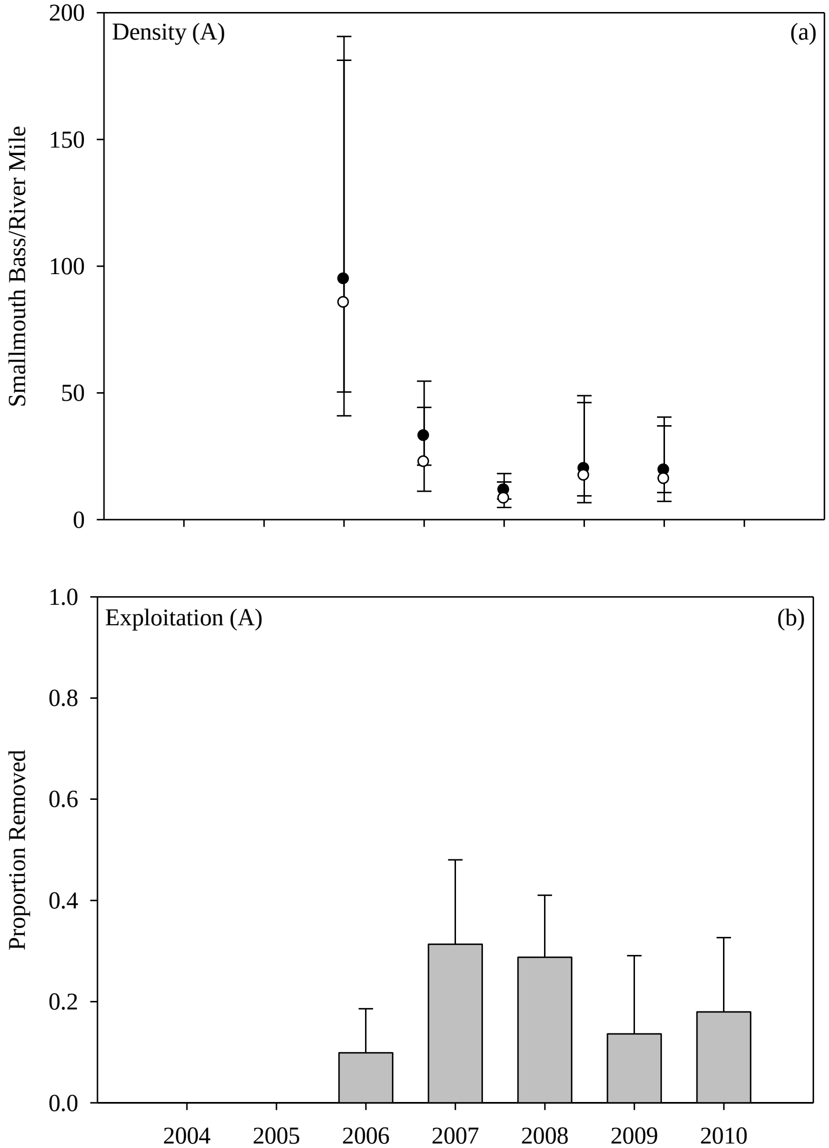


Figure 2. Pre-removal (filled circles) and post-removal (open circles) density (panel a) and exploitation rates (panel b) of adult smallmouth bass (*Micropterus dolomieu*) in the Colorado-Gunnison reach, Colorado and Gunnison rivers, Colorado, 2006–2010. Density error bars are asymmetric 95% confidence intervals; exploitation error bars are symmetric 95% confidence intervals (lower limit not shown). Smallmouth bass were removed in 2004-2005 but sufficient data were not available to produce density and exploitation estimates.

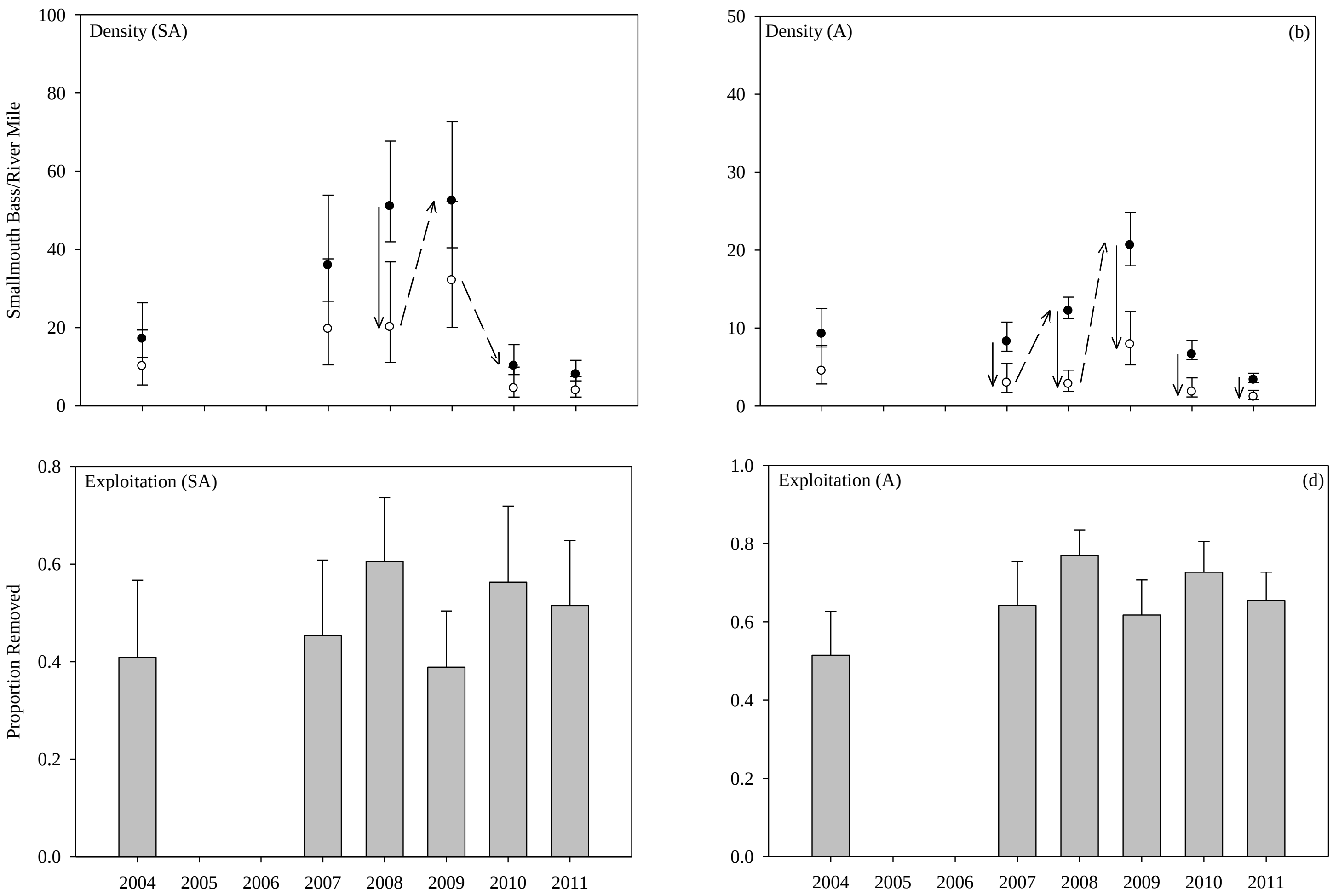


Figure 3. Pre-removal (filled circles) and post-removal (open circles) density (panel a) and exploitation rates (panel b) of sub-adult (SA) and adult (A) smallmouth bass (*Micropterus dolomieu*) in the Middle Green reach, Green River, Utah. Density error bars are asymmetric 95% confidence intervals; exploitation error bars are symmetric 95% confidence intervals (lower limit not shown). Arrows indicate statistically significant changes in density based on non-overlapping confidence intervals: solid arrows, pre- to post-removal; dashed arrows, post- to pre-removal. Sufficient data were not available from this reach to produce density and exploitation estimates for 2005 and 2006 (see text for more details).

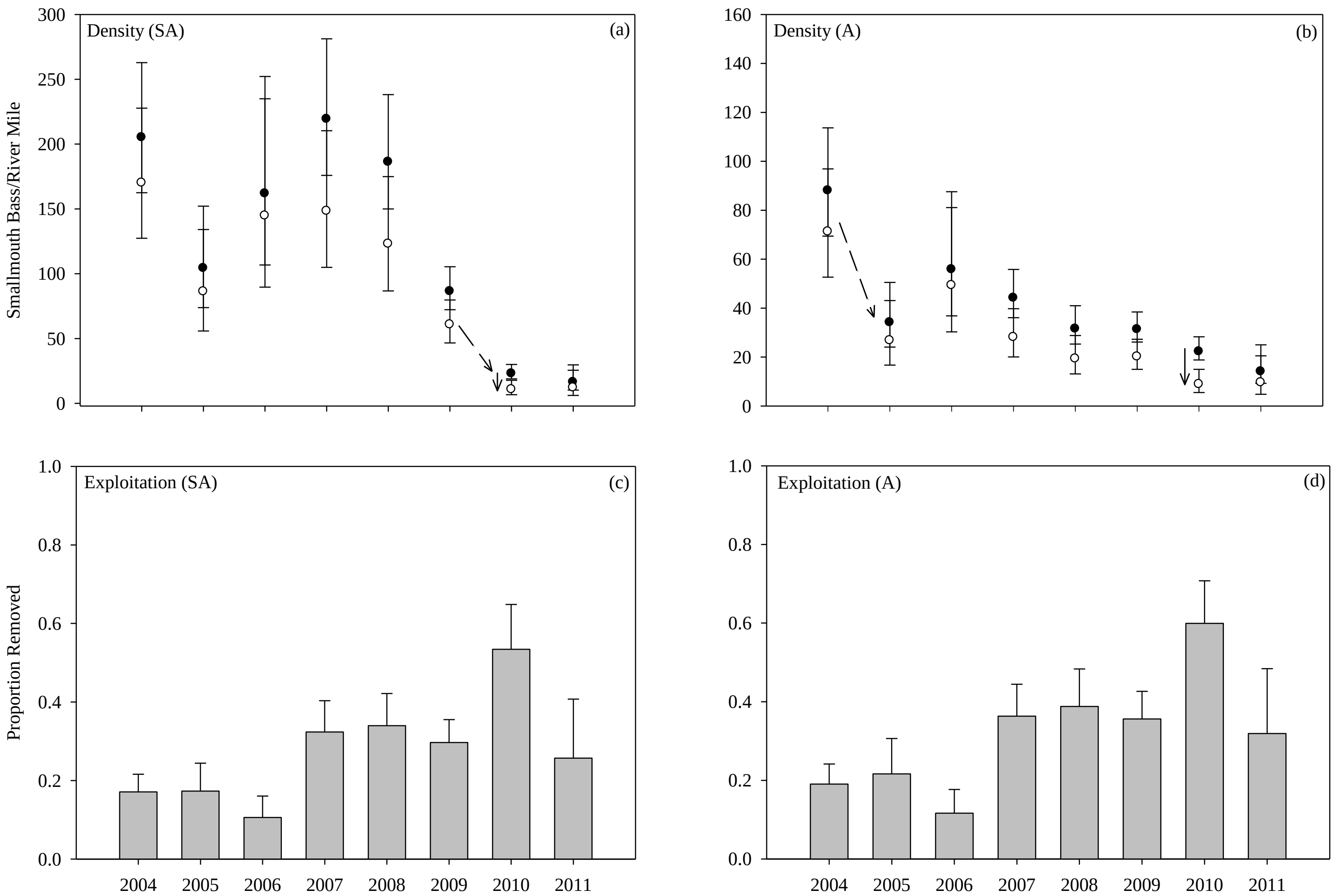


Figure 4. Pre-removal (filled circles) and post-removal (open circles) density (panel a) and exploitation rates (panel b) of sub-adult (SA) and adult (A) smallmouth bass (*Micropterus dolomieu*) in the Echo-Split reach, Green River, Colorado and Utah, 2004–2011. Density error bars are asymmetric 95% confidence intervals; exploitation error bars are symmetric 95% confidence intervals (lower interval not shown). Arrows indicate statistically significant changes in density based on non-overlapping confidence intervals: solid arrows, pre- to post- removal; dashed arrows, post- to pre-removal.

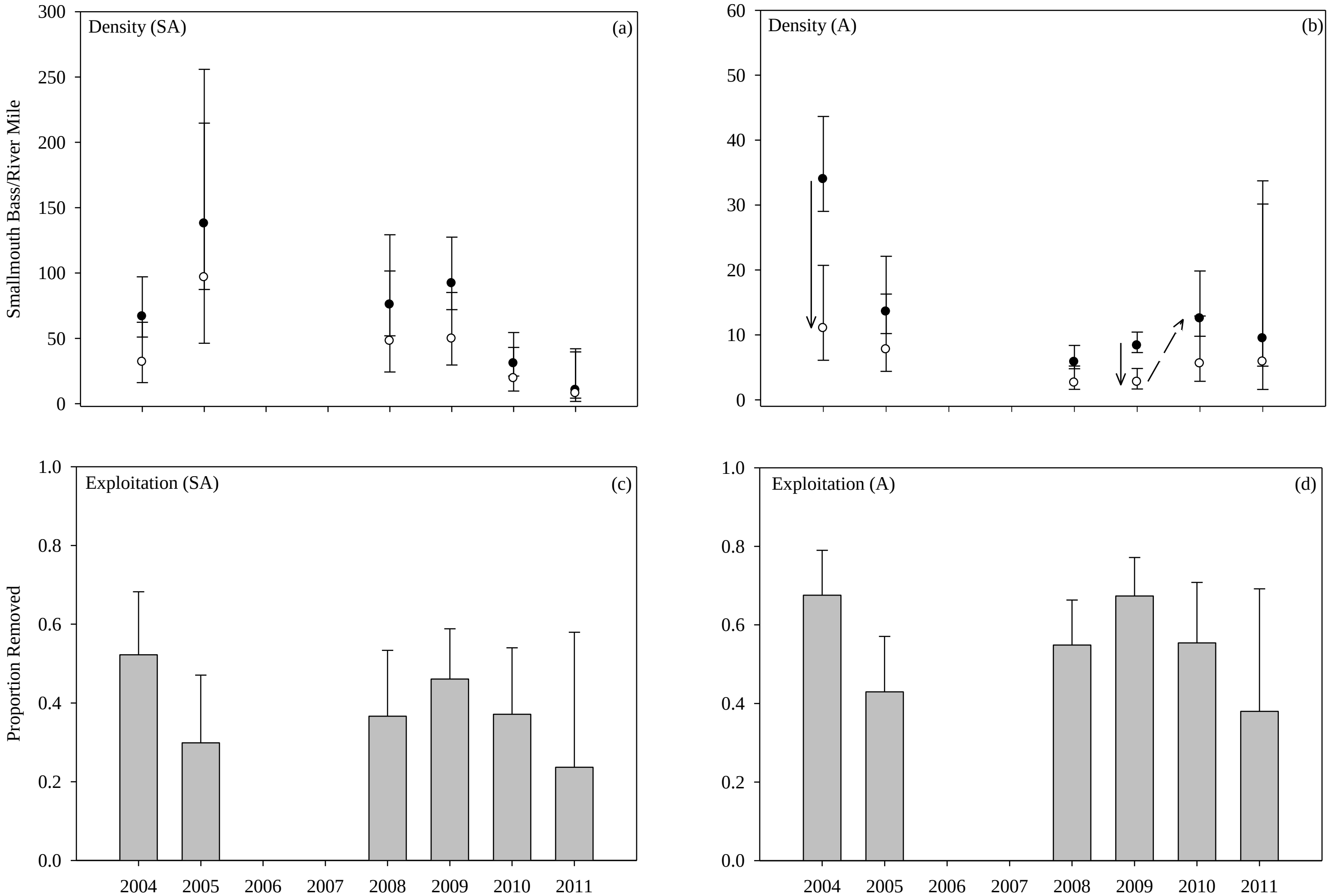


Figure 5. Pre-removal (filled circles) and post-removal (open circles) density (panel a) and exploitation rates (panel b) of sub-adult (SA) and adult (A) smallmouth bass (*Micropterus dolomieu*) in the Yampa Canyon reach, Yampa River, Colorado, 2004–2011. Density error bars are asymmetric 95% confidence intervals; exploitation error bars are symmetric 95% confidence intervals (lower limit not shown). Arrows indicate statistically significant changes in density based on non-overlapping confidence intervals: solid arrows, pre- to post- removal; dashed arrows, post- to pre-removal.

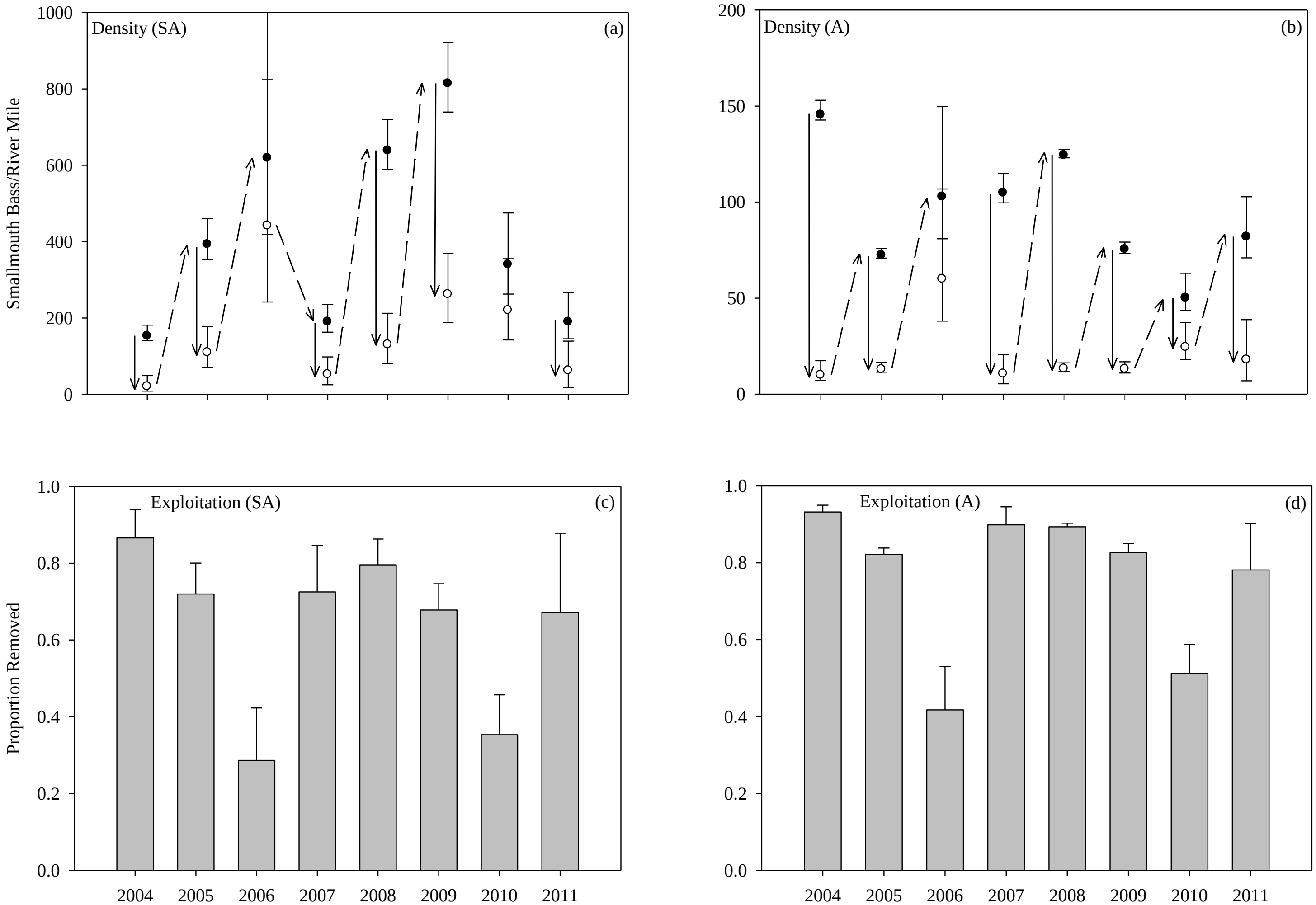


Figure 6. Pre-removal (filled circles) and post-removal (open circles) density (panel a) and exploitation rates (panel b) of sub-adult (SA) and adult (A) smallmouth bass (*Micropterus dolomieu*) in the Lily Park reach, Yampa River, Colorado, 2004–2011. Density error bars are asymmetric 95% confidence intervals; exploitation error bars are symmetric 95% confidence intervals (lower limit not shown). Arrows indicate statistically significant changes in density based on non-overlapping confidence intervals: solid arrows, pre- to post- removal; dashed arrows, post- to pre-removal.

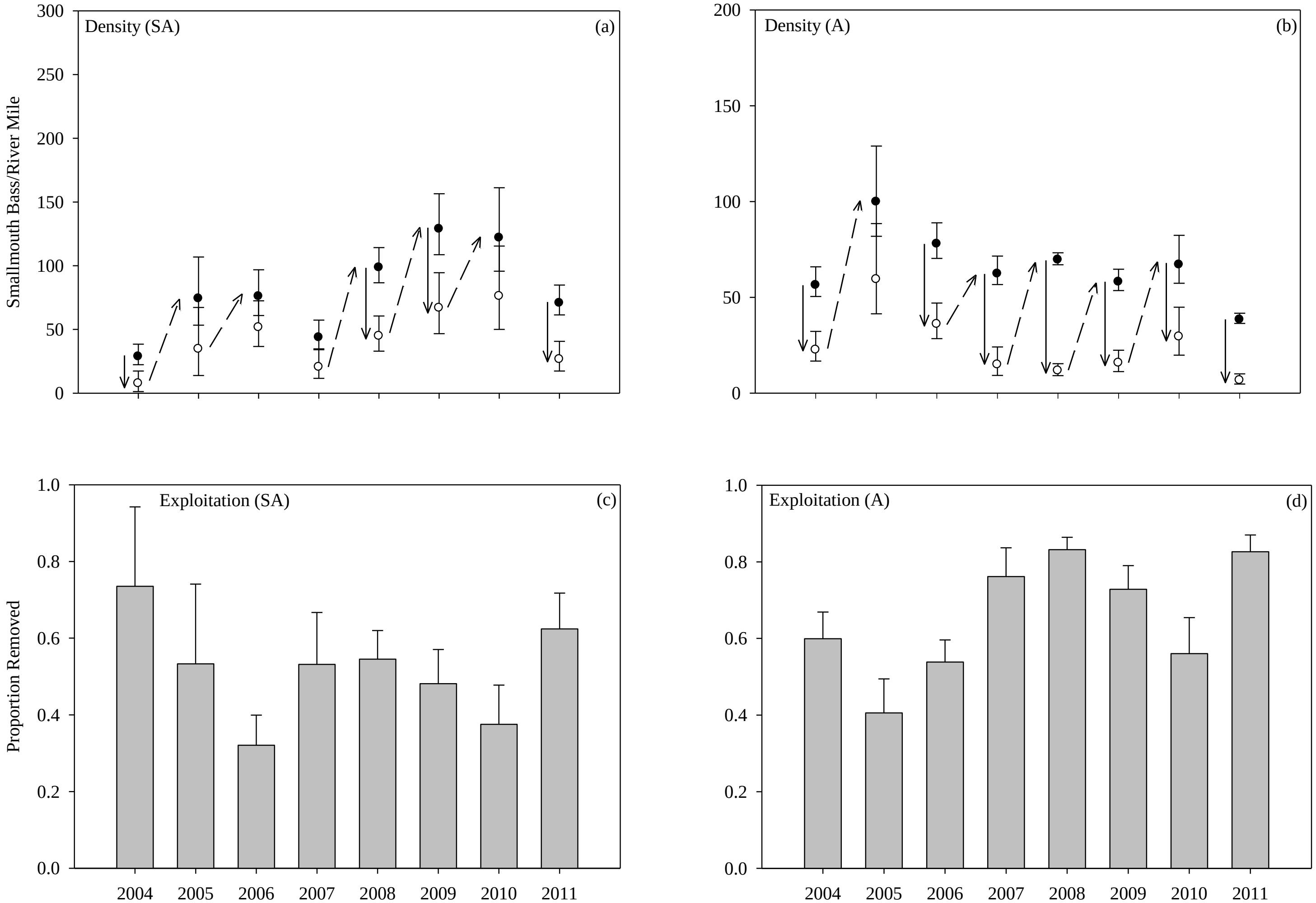


Figure 7. Pre-removal (filled circles) and post-removal (open circles) density (panel a) and exploitation rates (panel b) of sub-adult (SA) and adult (A) smallmouth bass (*Micropterus dolomieu*) in the Little Yampa Canyon reach, Yampa River, Colorado, 2004–2011. Density error bars are asymmetric 95% confidence intervals; exploitation error bars are symmetric 95% confidence intervals (lower limit not shown). Arrows indicate statistically significant changes in density based on non-overlapping confidence intervals: solid arrows, pre- to post- removal; dashed arrows, post- to pre-removal.

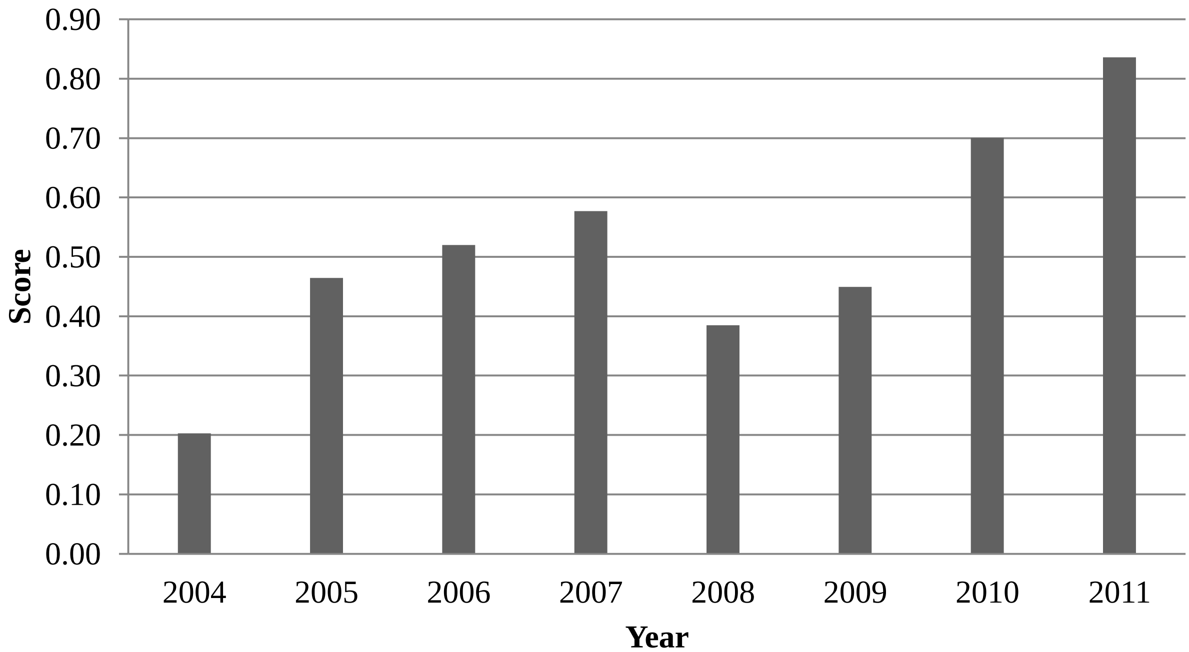


Figure 8. Weighted scores from a consequence table reflecting the effectiveness of removal and environmental factors on reducing the density of smallmouth bass (*Micropterus dolomieu*) in six reaches in the upper Colorado River basin, Colorado and Utah, from 2004 to 2011.

Appendix 1. Estimates of von Bertalanffy growth function parameters daily growth rate (k; mm) and asymptotic length ($\hat{L}_{\infty}$) for smallmouth bass (*Micropterus dolomieu*) captured in six reaches of the upper Colorado River basin, 2004-2011. The coefficient of determination (r^2) is from a regression of observed recapture lengths as a function of predicted recapture lengths from the von Bertalanffy growth function for the six focal reaches. In the model, fish were only allowed to grow on days when water temperatures were at or above 20º C.

River†	Reach	$\hat{k}$	$\widehat{SE}$	$\hat{L}_{\infty}$	$\widehat{SE}$	r^2
GR	Middle Green	0.00145	0.00039	716	136	0.976
GR	Echo-Split	0.00486	0.00099	443	52	0.950
YA	Yampa Canyon	0.00136	0.00060	590	172	0.989
YA	Lily Park	0.00116	0.00356	800	1776	0.997
YA	Little Yampa Canyon	0.00305	0.00030	478	22	0.998

† GR, Green River; YA, Yampa River.

Appendix 2. Counts of smallmouth bass (*Micropterus dolomieu*) removed, including translocated fish, by all gear types and sampling strategies (e.g., numbered passes, high density areas) from the Colorado and Gunnison rivers from 2003-2011. Age allocation was determined by capture or recapture length just prior to removal. The lower 3.7 rkm (2.3 rmi) section of the Gunnison River was sampled as part of the effort to sample the Colorado River in all years (except 2003), elsewhere in the manuscript data from these two rivers are combined (2004-2011).

								Age & Size Class				
		Start	Duration	Elect. Effort		River Mile		Juvenile	Sub-adult	Adult	Unknown	
Reach	**Year**	**(m/d)**	**(days)**	**#p (hrs)†**	**Priority‡**	**Start**	**End**	**(<100 mm)**	**(100-199 mm)**	**(≥200 mm)**	**Age**	**Total**
Colorado River	2003	6/30	115	5 (89)	CC	171	132	19	105	46	5	175
Colorado River	2004	7/6	54	4 (182)	SM	240.5	127.5	94	567	412	1	1074
Colorado River	2005	7/12	45	4 (202)	SM	240.5	127.6	300	383	820	0	1503
Colorado River	2006	7/5	77	5 (208)	SM	240.4	127.6	288	53	459	0	800
Colorado River	2007	6/20	106	9 (411)	SM	248	127.6	1212	270	446	156	2084
Colorado River	2008	7/7	103	9 (420)	SM	248	127.5	378	242	156	0	776
Colorado River	2009	4/1	85	5 (450)	CS	193.7	0	1	7	78	0	86
Colorado River	2009	6/30	93	9 (454)	SM	240.4	132	209	136	174	0	519
Colorado River	2010	7/7	85	9 (467)	SM	240.4	127.6	2126	161	217	0	2504
Colorado River	2010	10/20	8	1 (4)	HB	213	205.5	0	0	0	1	1
Colorado River	2011	8/9	79	10 (510)	SM	240.4	136	300	785	173	1	1259
Gunnison River	2004	7/9	40	4 (12)	SM	3	0.7	1	55	59	0	115
Gunnison River	2005	7/27	31	4 (12)	SM	3	0.7	11	16	66	0	93
Gunnison River	2006	7/26	49	5 (11)	SM	3	0.7	0	1	22	0	23
Gunnison River	2007	7/20	71	9 (27)	SM	3	0.7	8	1	18	0	27
Gunnison River	2008	4/3	76	5 (21)	CS	3	0.7	3	0	11	0	14
Gunnison River	2008	8/6	70	7 (?)	SM	3	0.7	1	5	84	0	90
Gunnison River	2009	4/7	64	5 (10)	CS	3	0.8	0	1	10	0	11
Gunnison River	2009	7/29	51	9 (28)	SM	3	0.7	1	5	16	0	22
Gunnison River	2010	7/28	59	9 (31)	SM	3	0.7	37	1	14	0	52

Gunnison River	2011	8/11	71	9 (37)	SM	3	0.7	4	23	10	0	37
							Total	4993	2817	3291	164	**11265**

† #p (hrs), number of electrofishing passes (p) and hours of sampling measured by the electronic counter on electrofishing units: passes are performed using boat electrofishing and each pass encompasses both shorelines and the entire reach.

‡ The priority species for the sampling effort: HB = humpback chub (*Gila cypha*); CC = channel catfish (*Ictalurus punctatus*); SM = smallmouth bass; CS = Colorado pikeminnow (*Ptychocheilus lucius*). CC and SM were targeted for removal; CS and HB were released after being measured and fitted with a Passive Integrated Transponder tag (i.e., PIT-tag).

Appendix 3. Counts of smallmouth bass (*Micropterus dolomieu*) removed, including translocated fish, by all gear types and sampling strategies (e.g., numbered passes, high density areas) from the Green and White rivers from 2001-2011. Age allocation was determined by capture or recapture length just prior to removal. Echo-Split and Lodore-Echo refer to Echo Park to Split Mountain and Lodore Canyon to Echo Park, respectively.

								Age & Size Class				
		Start	Duration	Elect. Effort		River Mile		Juvenile	Sub-adult	Adult	Unknown	
Reach	Year	(m/d)	(days)	#p (hrs)†	Priority‡	Start	End	(<100 mm)	(100-199 mm)	(≥200 mm)	Age	Total
Desolation	2004	8/16	47	4 (143)	SM	216	132	16	278	645	0	939
Desolation	2005	7/24	56	4 (131)	SM	216	132	0	76	301	0	377
Desolation	2006	7/23	45	4 (62)	SM	216	132	9	24	104	0	137
Desolation	2010	9/4	39	3 (7)	HB	185.2	145.7	0	0	0	21	21
Middle Green	2001	3/19	103	0 (46)	SM	318	236	0	4	62	5	71
Middle Green	2001	4/16	52	?	CS	318	246	1	0	1	19	21
Middle Green	2002	4/2	171	0 (33)	NP	318	236	0	0	0	17	17
Middle Green	2003	3/13	107	0 (107)	NP	318	236	0	0	0	29	29
Middle Green	2004	3/22	85	0 (24)	NP	318	236	0	0	0	84	84
Middle Green	2004	4/30	119	4 (173)	SM	318	215	103	969	800	0	1872
Middle Green	2005	3/21	191	4 (163)	SM	318	215	45	230	397	18	690
Middle Green	2006	3/27	217	4 (221)	SM	318	215	360	380	230	0	970
Middle Green	2007	3/27	218	9 (261)	SM	318	247.9	2592	3011	980	0	6583
Middle Green	2008	3/26	213	12 (546)	SM	318	247.9	341	2257	1080	0	3678
Middle Green	2009	3/25	205	13 (470)	SM	319.3	215	219	1578	1529	0	3326
Middle Green	2010	4/8	197	11 (476)	SM	319.6	206.6	647	2409	1094	0	4150
Middle Green	2011	3/23	204	11 (553)	SM	333.9	206.6	195	1986	456	0	2637
Echo-Split	2004	8/3	45	4 (112)	SM	345.6	319.6	31	1405	904	0	2340
Echo-Split	2005	8/2	29	4 (84)	SM	345.6	319.6	27	385	290	1	703
Echo-Split	2006	7/18	52	5 (84)	SM	345.6	319.6	229	525	217	37	1008
Echo-Split	2007	7/2	87	15 (323)	SM	344	318	2090	2529	689	5973	11281
Echo-Split	2008	6/16	110	16 (324)	SM	345.6	319.6	632	2022	491	0	3145

Echo-Split	2009	6/20	101	16 (288)	SM	344.6	320	482	602	425	26	1535
Echo-Split	2010	6/21	109	15 (307)	SM	344.6	319.6	174	329	390	0	893
Echo-Split	2011	7/19	74	12 (215)	SM	344.6	319.6	41	118	127	0	286
Lodore-Echo	2002	7/9	66	2 (23)	All	356.9	334	6	57	27	0	90
Lodore-Echo	2003	7/21	60	2 (30)	All	359.9	334	6	76	181	86	349
Lodore-Echo	2004	7/26	60	2 (37)	All	363.5	334	2	81	194	34	311
Lodore-Echo	2005	8/2	59	2 (29)	All	361.1	334	1	22	44	73	140
Lodore-Echo	2006	7/10	67	2 (24)	All	363.6	334.1	47	37	72	3	159
Lodore-Echo	2007	7/9	74	2 (38)	All	363.7	334.2	193	265	102	1	561
Lodore-Echo	2008	7/21	52	2 (18)	All	360.5	336.3	0	30	32	6	68
Lodore-Echo	2009	7/20	66	1 (28)	All	363.6	334.4	2	106	62	0	170
Lodore-Echo	2010	7/19	46	1 (39)	All	363.7	334.3	1	50	85	0	136
Lodore-Echo	2011	8/9	45	1 (20)	All	363.6	334.4	0	3	42	0	45
White River	2010	4/12	4	1 (21)	3spp.	66.5	24	1	2	7	0	10
White River	2011	7/5	17	3 (139)	3spp.	66.5	24	0	6	2	0	8
							Total	8493	21852	12062	6433	48840

† #p (hrs), number of electrofishing passes (p) and hours of sampling measured by the electronic counter on electrofishing units: passes are performed using boat electrofishing and each pass encompasses both shorelines and the entire reach.

‡ The priority species for the sampling effort: NP = northern pike (*Esox lucius*); HB = humpback chub (*Gila cypha*); CC = channel catfish (*Ictalurus punctatus*); SM = smallmouth bass; CS = Colorado pikeminnow (*Ptychocheilus lucius*); All Species = an effort to sample the species community as a whole; 3spp. refers to three species of native sucker. CC, NP and SM were targeted for removal; CS and HB were released after being measured and fitted with a Passive Integrated Transponder tag (i.e., PIT-tag).

Appendix 4. Counts of smallmouth bass (*Micropterus dolomieu*) removed, including translocated fish, by all gear types and sampling strategies (e.g., numbered passes, high density areas) from the Yampa River from 2001-2011. Age allocation was determined by capture or recapture length just prior to removal when lengths were recorded.

								Age & Size Class				
		Start	Duration	Elect. Effort		River Mile		Juvenile	Sub-adult	Adult	Unknown	
Reach	Year	(m/d)	(days)	#p (hrs)†	Priority‡	Start	End	(<100 mm)	(100-199 mm)	(≥200 mm)	Age	Total
Yampa Canyon	2001	6/11	75	5 (87)	CC	45	0	0	1	2	4	7
Yampa Canyon	2002	5/28	87	4 (43)	CC	45	0	0	9	4	305	318
Yampa Canyon	2003	6/23	38	4 (58)	CC	45	0	0	116	83	114	313
Yampa Canyon	2004	4/14	100	8 (122)	SM	45	0	365	1490	1132	2	2989
Yampa Canyon	2005	6/13	47	5 (172)	SM	45	0	109	1824	326	0	2259
Yampa Canyon	2006	6/5	116	6 (179)	SM	45	0	96	800	759	276	1931
Yampa Canyon	2007	6/5	24	4 (112)	SM	45	0	43	374	251	222	890
Yampa Canyon	2008	7/8	25	4 (155)	SM	45	0	338	1807	211	47	2403
Yampa Canyon	2009	4/7	102	7 (200)	SM	46.3	0.5	109	1919	287	0	2315
Yampa Canyon	2010	6/1	46	6 (179)	SM	46.3	0	36	491	362	0	889
Yampa Canyon	2011	7/5	39	6 (183)	SM	45	0	79	111	181	0	371
Lily Park	2003	4/30	57	4 (28)	NP	55.6	44.8	0	0	0	0	0
Lily Park	2004	4/24	75	6 (26)	SM	55.3	51	160	558	606	0	1324
Lily Park	2005	5/4	77	6 (35)	SM	55.5	50.5	142	1431	313	0	1886
Lily Park	2006	4/25	57	6 (37)	SM	55.4	49.5	186	1080	259	4	1529
Lily Park	2007	4/17	104	6 (40)	SM	55.6	50.3	469	818	552	127	1966
Lily Park	2008	4/22	78	9 (83)	SM	55.3	50	1489	2774	598	0	4861
Lily Park	2009	4/28	71	8 (97)	SM	55.6	47.5	559	4920	625	14	6118
Lily Park	2010	4/13	76	8 (71)	SM	55.5	47	473	1092	277	221	2063
Lily Park	2011	5/10	90	7 (71)	SM	55.8	47.5	272	1130	577	0	1979
Cross Mt	2007	8/14	2	0 (0)	All	58.5	55.3	0	0	0	116	116
Cross Mt	2008	9/25	5	0 (0)	All	58.5	55.3	0	0	0	37	37

Sunbeam	2005	5/4	63	4 (27)	NP	71	58.5	0	0	0	0	0
Sunbeam	2006	5/2	47	4 (29)	NP	71	58.5	0	0	0	0	0
Sunbeam	2007	4/24	52	4 (32)	NP	71	58.5	0	0	0	0	0
Sunbeam	2008	4/19	49	4 (32)	NP	71	58.5	3	2	0	0	5
Sunbeam	2009	4/24	48	4 (36)	NP	71	58.5	36	40	29	0	105
Sunbeam	2010	4/26	45	4 (32)	NP	71	58.5	2	15	7	0	24
Sunbeam	2011	5/2	57	4 (39)	NP	71.8	58.5	2	15	7	0	24
Lower Maybell	2005	5/19	42	4 (29)	NP	79.2	71	0	0	0	0	0
Lower Maybell	2006	4/18	57	5 (34)	NP	79.2	71	0	0	0	0	0
Lower Maybell	2007	4/17	50	4 (31)	NP	79.2	71	0	0	0	0	0
Lower Maybell	2008	4/17	49	4 (35)	NP	79.2	71	6	4	0	0	10
Lower Maybell	2009	4/14	50	4 (34)	NP/SM	79.2	71	34	111	30	0	175
Lower Maybell	2010	4/13	42	5 (36)	NP/SM	79.2	71	3	10	13	0	26
Lower Maybell	2011	4/29	61	4 (30)	NP/SM	79.2	71	12	30	21	0	63
Upper Maybell	2005	5/5	63	5 (31)	NP	88.7	81.6	0	0	0	0	0
Upper Maybell	2006	4/18	59	4 (34)	NP	88.7	79.2	0	0	0	0	0
Upper Maybell	2007	4/18	56	4 (37)	NP	88.7	79.2	2	5	4	0	11
Upper Maybell	2008	4/22	64	8 (73)	NP	88.7	79.2	309	468	421	0	1198
Upper Maybell	2009	4/16	55	7 (63)	NP	88.7	79.2	126	942	418	0	1486
Upper Maybell	2010	4/15	72	9 (67)	NP	88.7	79.2	177	474	224	0	875
Upper Maybell	2011	4/28	63	6 (54)	NP	88.7	79.2	46	267	185	0	498
Juniper Canyon	2010	9/5	1	0 (0)	SM	89.7	89.3	0	222	115	0	337
Juniper	2005	4/28	64	5 (36)	NP	100	91	0	0	2	0	2
Juniper	2006	4/26	52	4 (36)	NP	100	91	0	0	1	0	1
Juniper	2007	4/20	49	4 (37)	NP	100	91	0	0	1	0	1
Juniper	2008	4/18	57	4 (41)	SM	100	91	16	9	0	0	25
Juniper €	2009	4/15	91	5 (49)	SM	100	91	47	105	148	0	300
Juniper €	2010	4/14	87	8 (55)	SM	100	91	123	113	105	0	341
Juniper €	2011	4/27	117	7 (53)	SM	100	91	136	70	72	0	278
LYC & Juniper	2003	4/24	70	6 (215)	NP	119.9	90.5	4	123	179	0	306
LYC	2004	4/22	78	9 (195)	SM	124	100	55	123	181	0	359

LYC	2005	4/22	91	9 (220)	SM	124	100	249	529	827	0	1605
LYC	2006	4/20	86	7 (211)	SM	124	100	2359	1250	1005	7506	12120
LYC	2007	4/18	145	8 (193)	SM	124	100	2623	817	1056	5836	10332
LYC	2008	4/15	146	7 (295)	SM	124	100	2929	1186	1231	4403	9749
LYC	2009	4/7	166	11 (301)	SM	124	100	3979	1854	1477	5318	12628
LYC	2010	4/15	157	10 (284)	SM	124	100	2762	1744	1141	5462	11109
LYC	2011	4/26	118	14 (407)	SM	124	100	1755	1183	839	1876	5653
South Beach, & Juniper	2004	4/21	77	6 (111)	NP	135.3	90.5	0	0	1	0	1
South Beach	2005	4/26	64	6 (51)	NP	139.2	124	0	0	0	0	0
South Beach	2006	4/27	49	4 (41)	NP	134.2	124	19	126	198	2	345
South Beach	2007	4/19	56	4 (63)	SM	134.2	124	75	114	351	1	541
South Beach	2008	4/21	84	8 (71)	SM	134.2	124	125	98	157	0	380
South Beach €	2009	4/17	84	7 (69)	SM	134.2	124	27	142	173	0	342
South Beach €	2010	4/16	77	13 (102)	SM	134.4	124	35	218	287	0	540
South Beach €	2011	4/11	133	10 (94)	SM	134.5	124	161	250	268	0	679
Hayden to Craig	2002	4/11	72	0 (0)	NP	197	139	0	0	0	0	0
Hayden to Craig	2003	5/13	50	3 (58)	NP	177.5	139.7	0	0	0	0	0
Hayden to Craig	2004	4/27	45	6 (183)	NP	170.9	134	1	5	307	1	314
Hayden to Craig	2005	4/18	53	7 (203)	NP	170	134	0	1	2	0	3
Hayden to Craig	2006	4/18	60	7 (159)	NP	170.9	134	0	0	2	1	3
Hayden to Craig	2007	4/30	32	7 (141)	NP	170.9	134	0	0	2	0	2
Hayden to Craig	2008	4/21	74	?	NP	171	136.9	0	0	0	0	0
Hayden to Craig	2009	4/20	46	7 (197)	NP	171	135	0	1	6	0	7
Hayden to Craig	2010	4/26	60	10 (233)	NP	171	134.2	5	29	34	0	68
Hayden to Craig	2011	4/25	82	7 (200)	NP	171	135	0	104	418	0	522
Craig €	2011	7/19	18	4 (14)	SM	139.9	134.5	31	22	26	0	79
							Total	26958	36711	20213	41047	**124929**

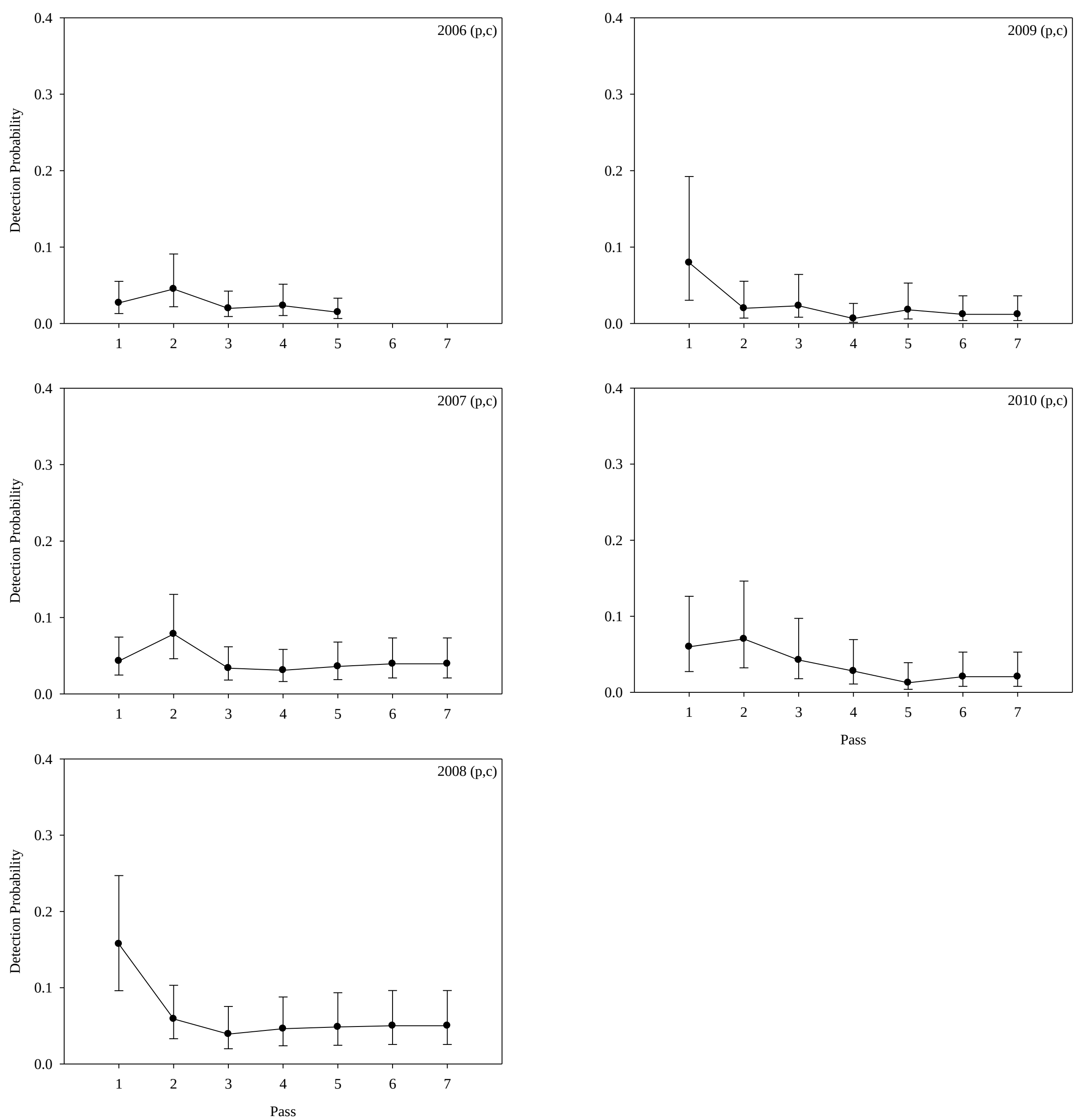
† #p (hrs), number of electrofishing passes (p) and hours of sampling measured by the electronic counter on electrofishing units: passes are performed using boat electrofishing and each pass encompasses both shorelines and the entire reach.

‡ The priority species for the sampling effort: CC = channel catfish (*Ictalurus punctatus*); NP = northern pike (*Esox lucius*); SM = smallmouth bass; All Species = an effort to sample the species community as a whole. CC, NP and SM were targeted for removal.

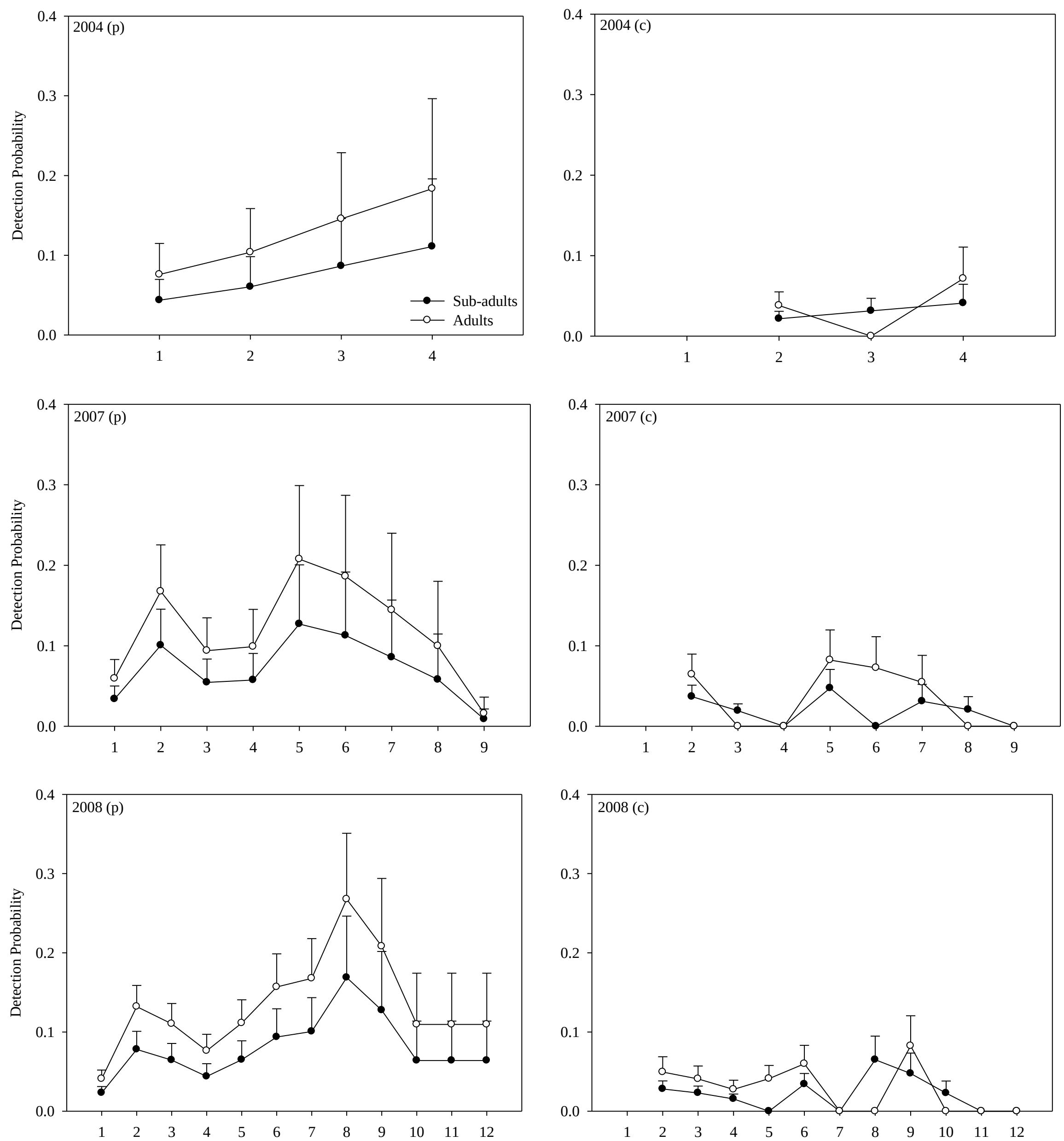
*Cross Mountain Canyon was sampled by angling, back-pack electrofishing and seine, there were no numbered passes and coverage was incomplete (Aaron Webber pers. comm.). Fish size was not provided in the RIP reports.

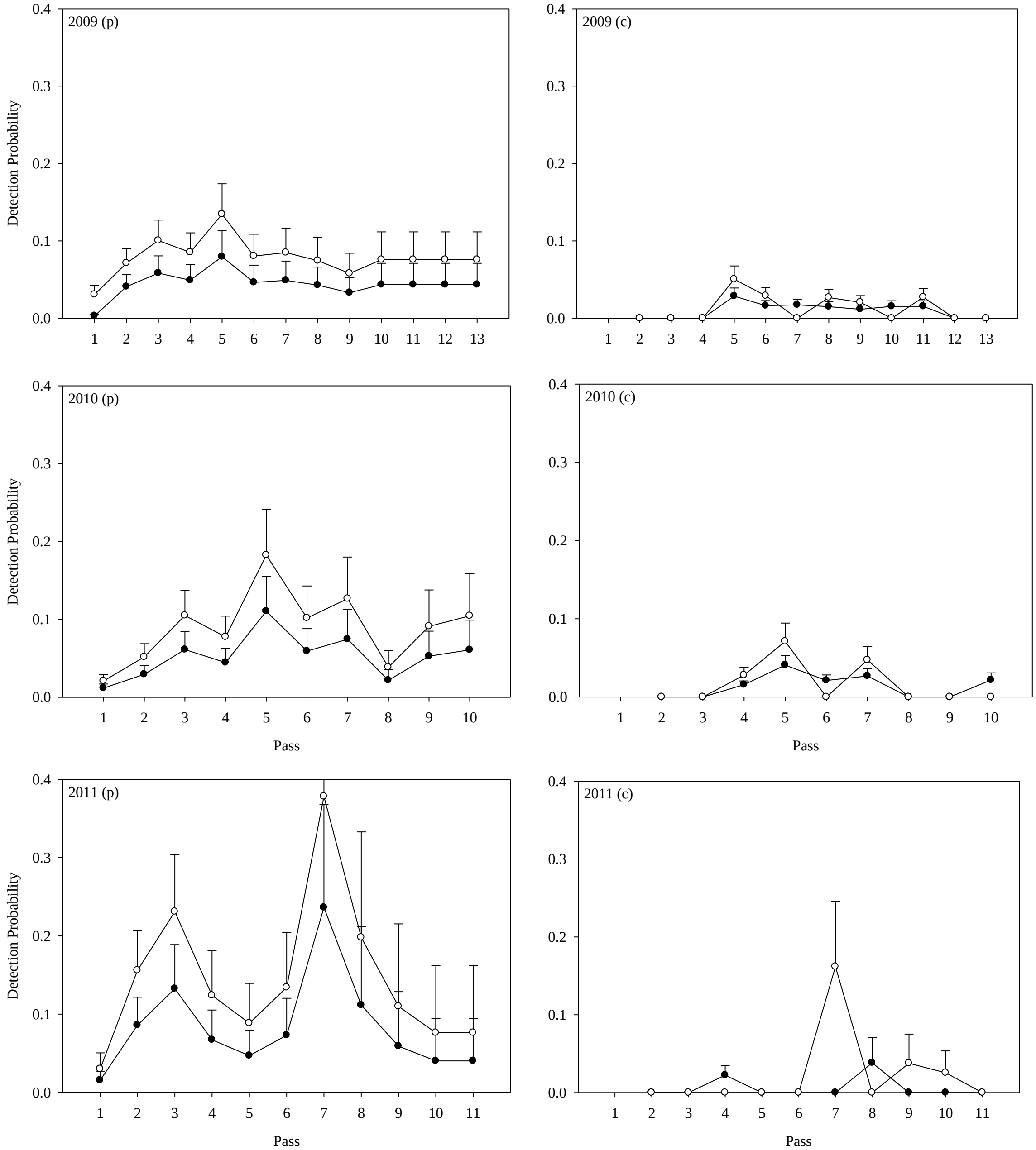
€ Removal counts in these years and reaches were affected by a mid-summer increase in boat electrofishing effort (the "surge").

Appendix 5. Estimates of adult smallmouth bass (*Micropterus dolomieu*) capture (p) and recapture probabilities (c) as a function of year and pass for the Colorado-Gunnison reach, Colorado and Gunnison Rivers, Colorado, 2006–2010. Figures include symmetrical 95% confidence intervals. Recapture probabilities were fixed to zero for some passes (not shown in figures) rather than estimated because no fish were recaptured on these passes and fixing these parameters improved AIC_c model support.

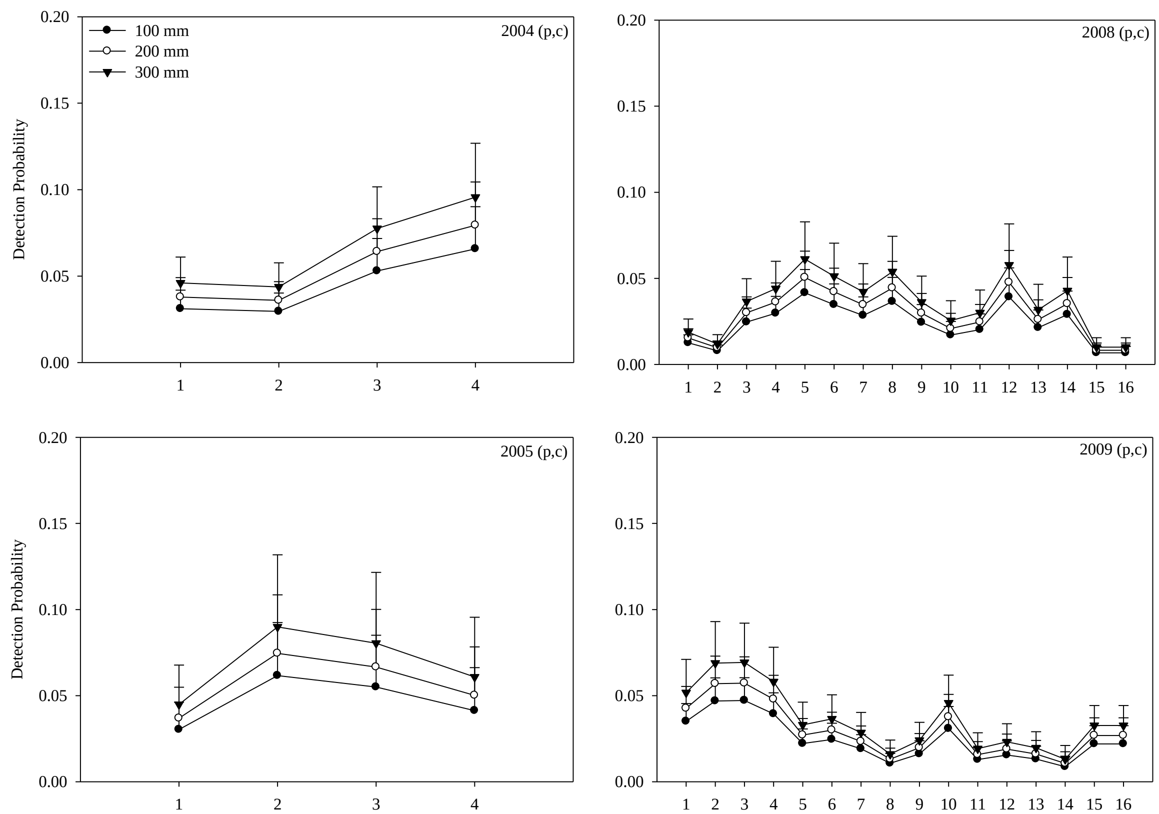


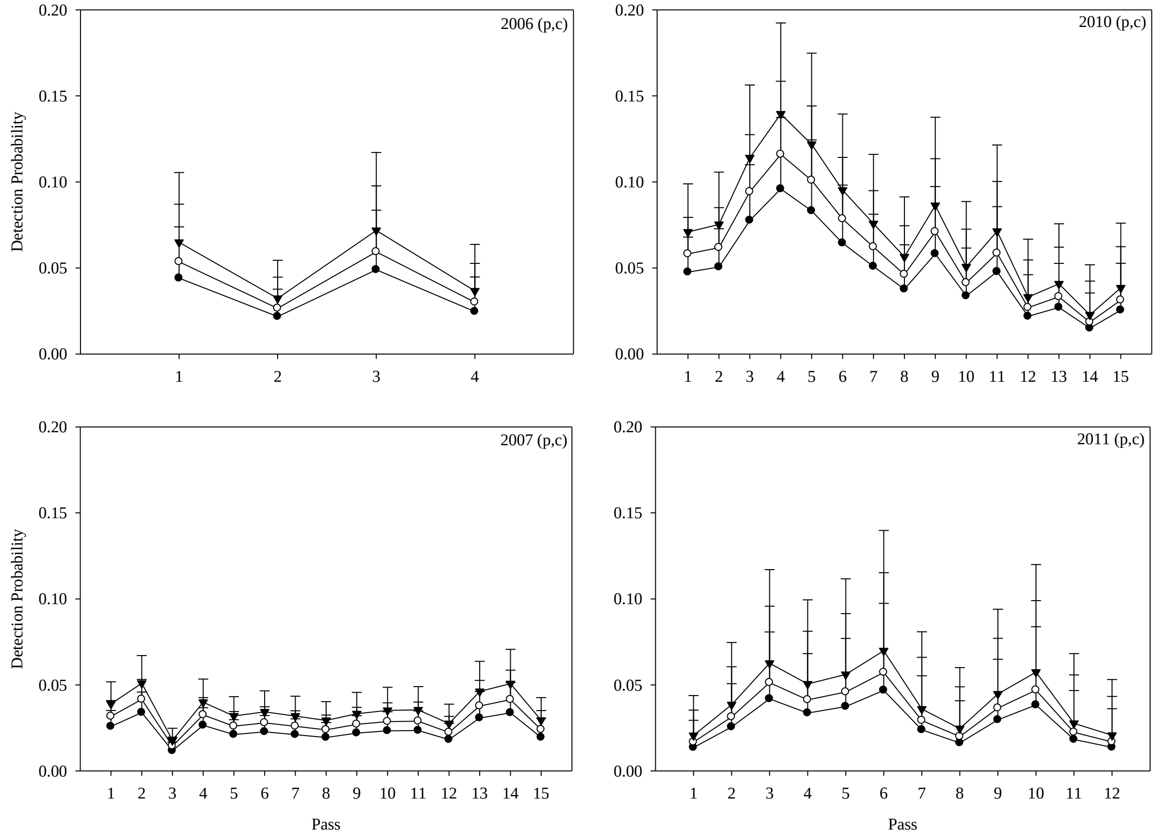
Appendix 6. Estimates of adult smallmouth bass (*Micropterus dolomieu*) capture (*p*) and recapture probabilities (*c*) as a function of year, pass, behavior and sub-adult and adult life stages from the Middle Green reach, Green River, Utah, 2004–2011. Recapture probabilities that equal zero were fixed in the model rather than estimated because no fish were recaptured on these passes and fixing these parameters improved AIC$_c$ model support. Figures include symmetrical 95% confidence intervals (lower limit not shown).



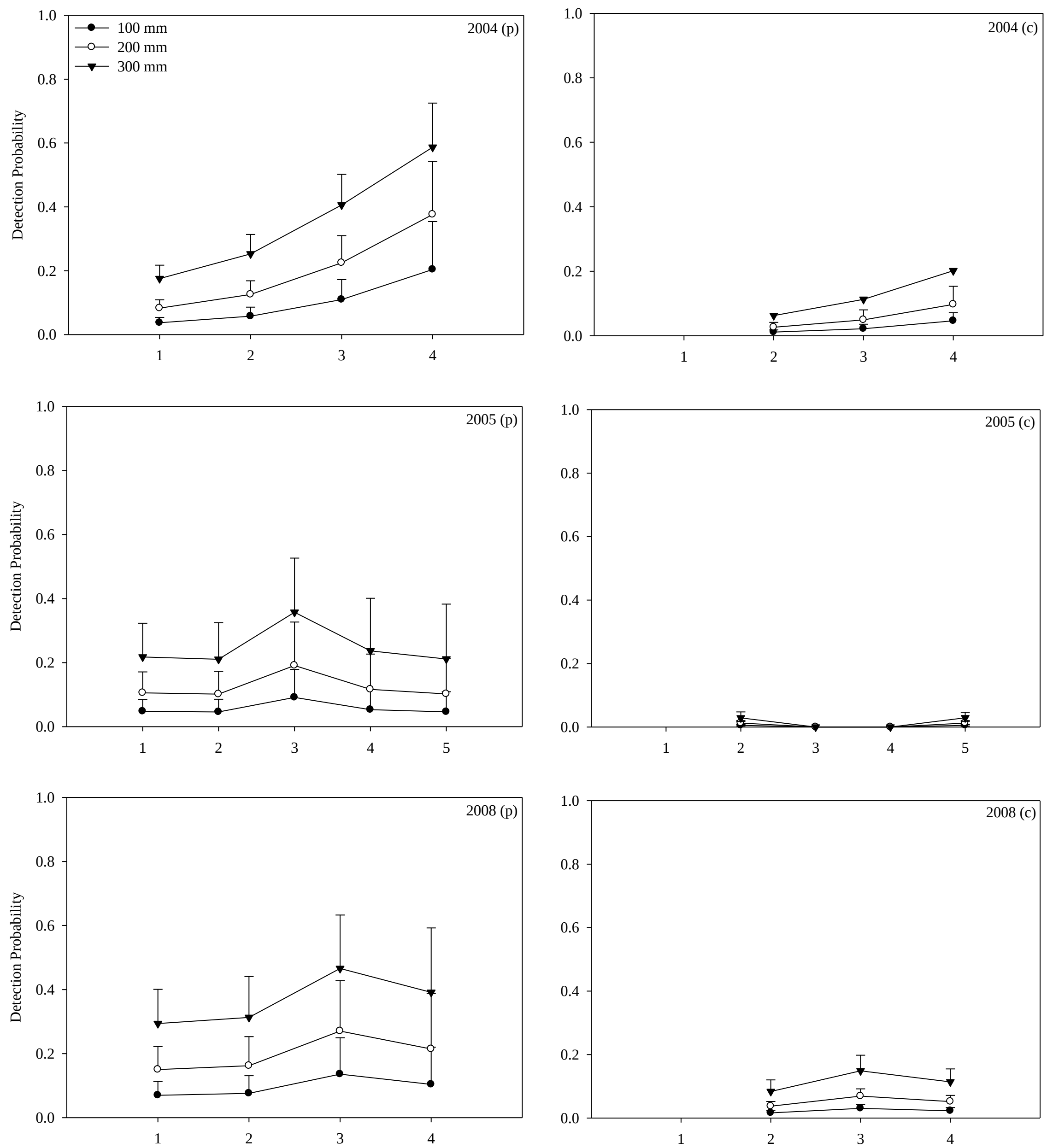

2009 (p)
2009 (c)
2010 (p)
2010 (c)
2011 (p)
2011 (c)
Detection Probability
Pass
0.0
0.1
0.2
0.3
0.4

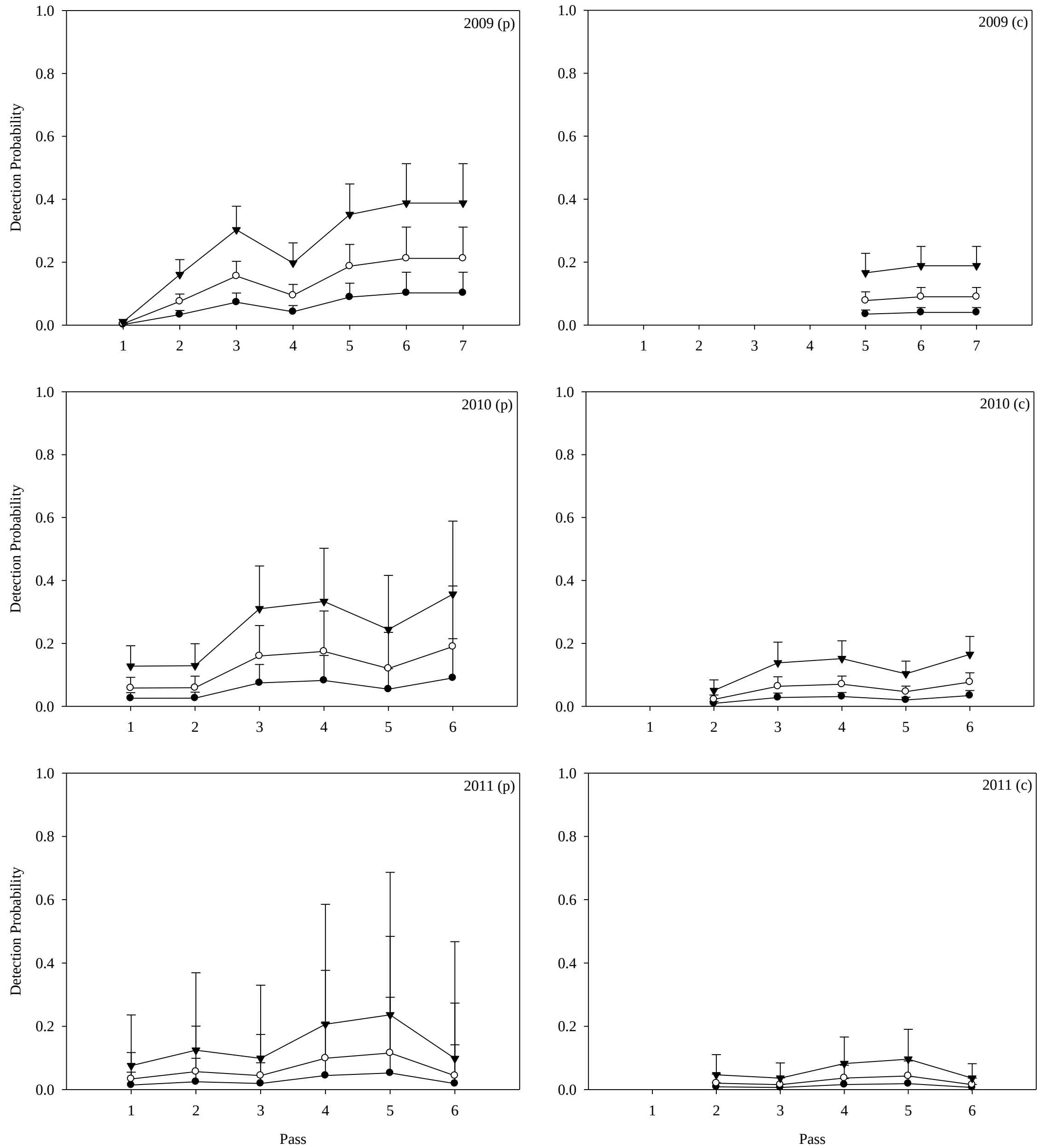
Appendix 7. Estimates of adult smallmouth bass (*Micropterus dolomieu*) capture (*p*) and recapture probabilities (*c*) as a function of year, pass and length (100, 200 and 300 mm) from the Echo Park to Split Mountain reach, Green River, Colorado and Utah, 2004–2011. Figures include symmetrical 95% confidence intervals (lower limit not shown). Recapture probabilities were fixed to zero for some passes (not shown in figures) rather than estimated because no fish were recaptured on these passes and fixing these parameters improved AIC_c model support.



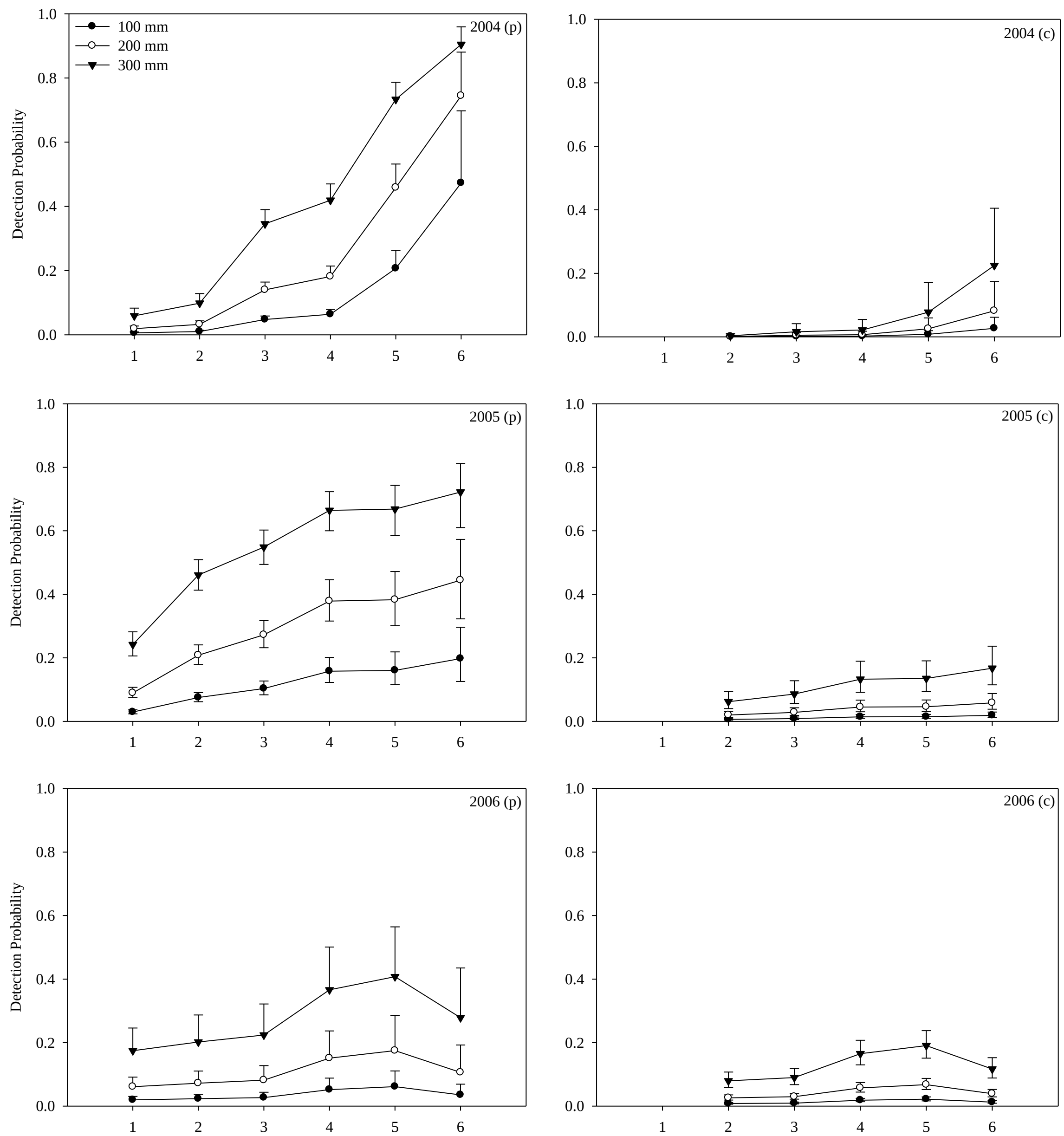

2006 (p,c)
2010 (p,c)
2007 (p,c)
2011 (p,c)
Detection Probability
Pass
0.00
0.05
0.10
0.15
0.20

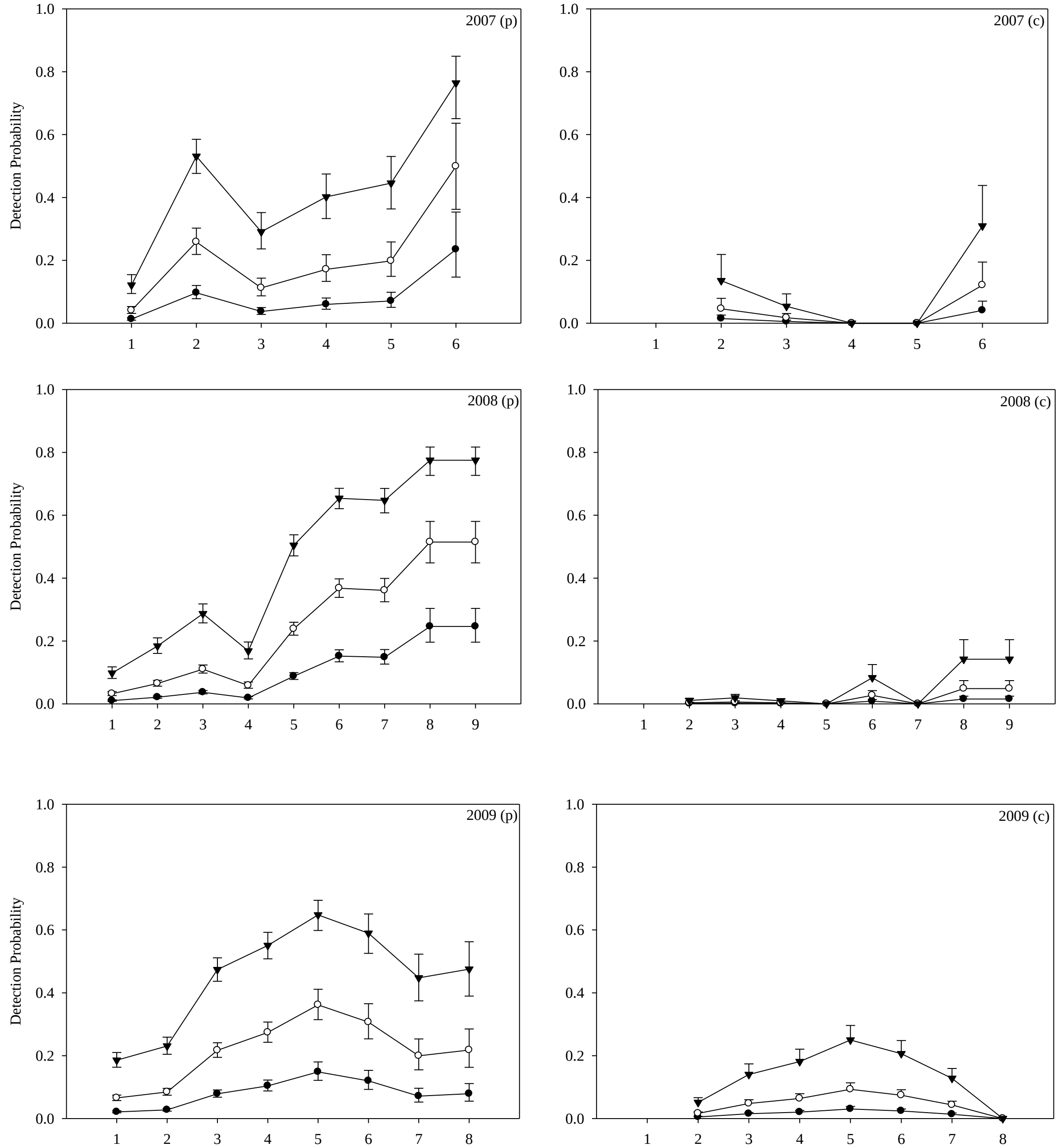
Appendix 8. Estimates of adult smallmouth bass (*Micropterus dolomieu*) capture (*p*) and recapture probabilities (*c*) as a function of year, pass, behavior and (total) fish length from Yampa Canyon, Yampa River, Colorado, 2004–2011. Recapture probabilities that equal zero were fixed in the model rather than estimated because no fish were recaptured on these passes and fixing these parameters improved AIC_c model support. Marking was not always conducted on pass one as implied by recapture probabilities. Figures include symmetrical 95% confidence intervals (lower limit not shown).

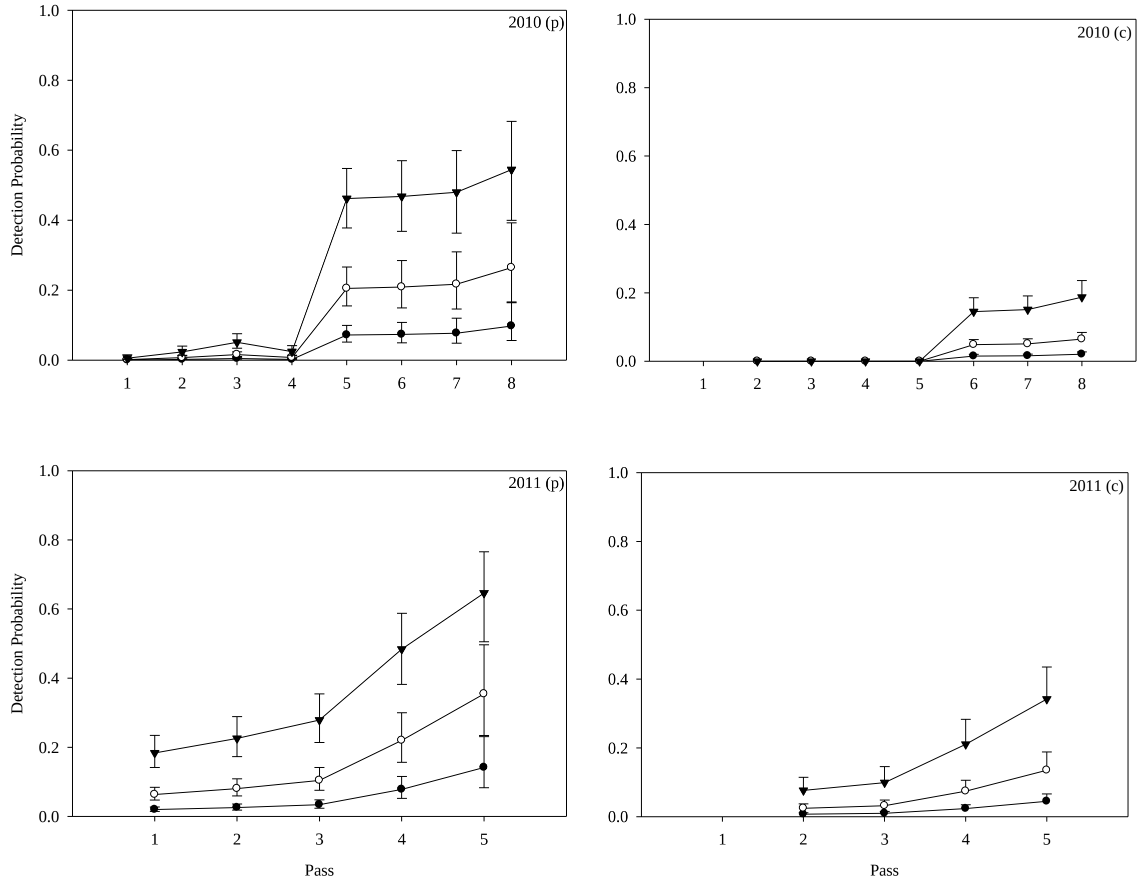



2009 (p)
2009 (c)
2010 (p)
2010 (c)
2011 (p)
2011 (c)
Detection Probability
Pass
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
5
6
7

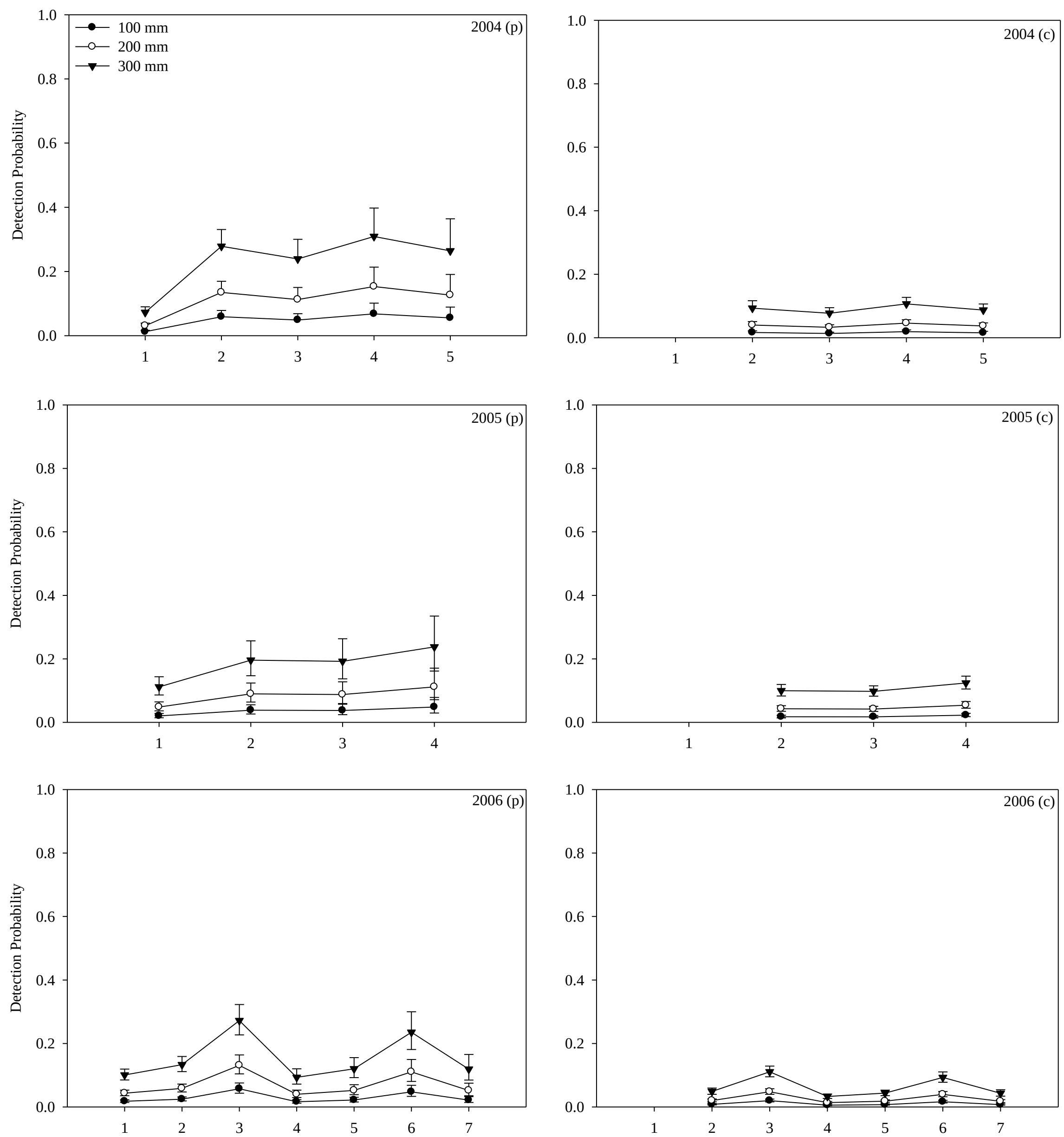
Appendix 9. Estimates of adult smallmouth bass (*Micropterus dolomieu*) capture (*p*) and recapture probabilities (*c*) as a function of year, pass, behavior and total fish length from Lily Park, Yampa River, Colorado, 2004–2011. Recapture probabilities that equal zero were fixed in the model rather than estimated because no fish were recaptured on these passes and fixing these parameters improved AIC$_c$ model support. Marking was not always conducted on pass one as implied by recapture probabilities. Figures include symmetrical 95% confidence intervals (lower limit not shown in some cases).

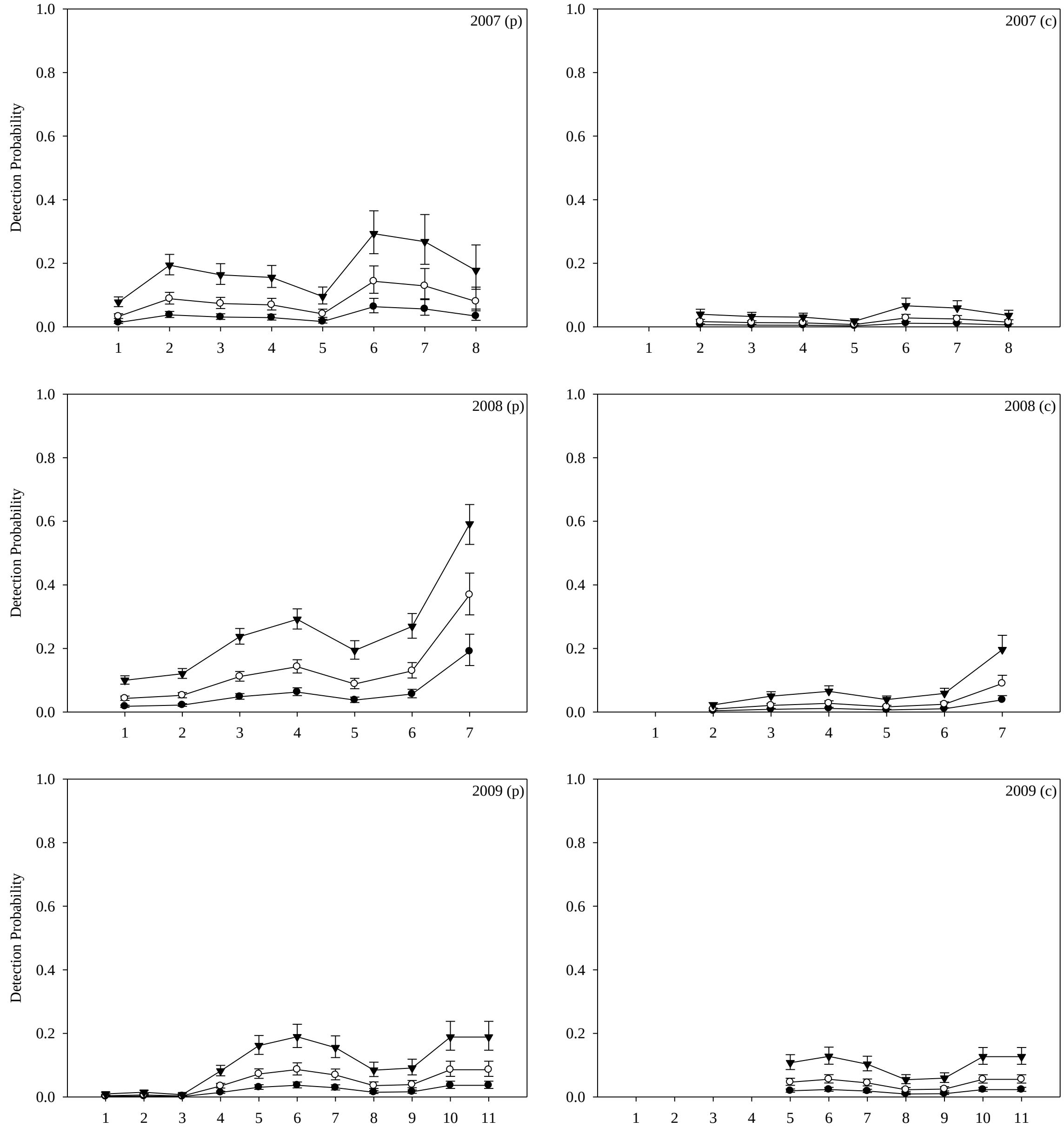


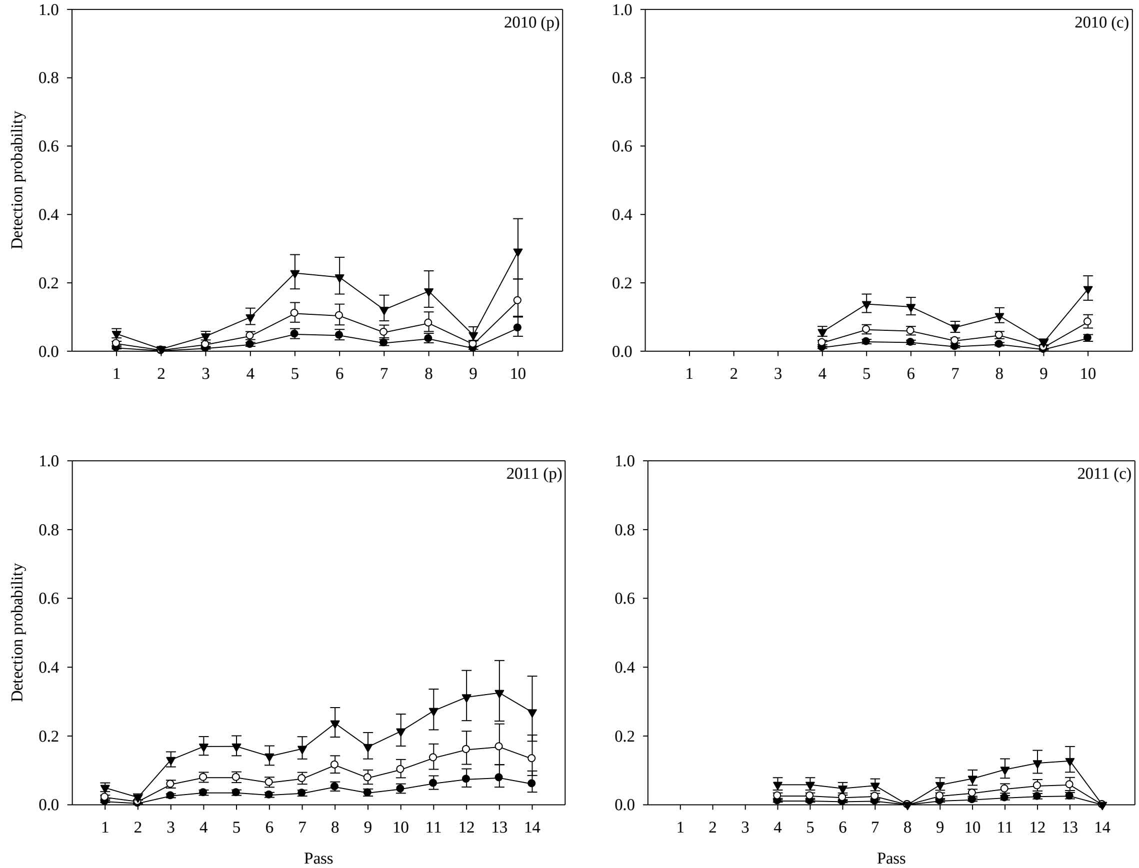

Detection Probability
2007 (p)
2007 (c)
2008 (p)
2008 (c)
2009 (p)
2009 (c)
0.0
0.2
0.4
0.6
0.8
1.0
1 2 3 4 5 6
1 2 3 4 5 6 7 8 9
1 2 3 4 5 6 7 8


2010 (p)
2010 (c)
2011 (p)
2011 (c)
Detection Probability
Detection Probability
Pass
Pass
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
5
6
7
8

Appendix 10. Estimates of adult smallmouth bass (*Micropterus dolomieu*) capture (*p*) and recapture probabilities (*c*) as a function of year, pass, behavior and (total) fish length from Little Yampa Canyon, Yampa River, Colorado, 2004–2011. Recapture probabilities that equal zero were fixed in the model rather than estimated because no fish were recaptured on these passes and fixing these parameters improved AIC_c model support. Marking was not always conducted on pass one as implied by recapture probabilities. Figures include symmetrical 95% confidence intervals.




2007 (p)
2007 (c)
2008 (p)
2008 (c)
2009 (p)
2009 (c)
Detection Probability
0.0
0.2
0.4
0.6
0.8
1.0
1 2 3 4 5 6 7 8
1 2 3 4 5 6 7
1 2 3 4 5 6 7 8 9 10 11


2010 (p)
2010 (c)
2011 (p)
2011 (c)
Detection probability
Pass
0.0
0.2
0.4
0.6
0.8
1.0