Correcting Length–Frequency Distributions for Imperfect Detection

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Abstract

Sampling gear selects for specific sizes of fish, which may bias length-frequency distributions that are commonly used to assess population size structure, recruitment patterns, growth, and survival. To properly correct for sampling biases caused by gear and other sources, length-frequency distributions need to be corrected for imperfect detection. We describe a method for adjusting length-frequency distributions when capture and recapture probabilities are a function of fish length, temporal variation, and capture history. The method is applied to a study involving the removal of Smallmouth Bass *Micropterus dolomieu* by boat electrofishing from a 38.6-km reach on the Yampa River, Colorado. Smallmouth Bass longer than 100 mm were marked and released alive from 2005 to 2010 on one or more electrofishing passes and removed on all other passes from the population. Using the Huggins mark–recapture model, we detected a significant effect of fish total length, previous capture history (behavior), year, pass, year × behavior, and year × pass on capture and recapture probabilities. We demonstrate how to partition the Huggins estimate of abundance into length frequencies to correct for these effects. Uncorrected length frequencies of fish removed from Little Yampa Canyon were negatively biased in every year by as much as 88% relative to mark–recapture estimates for the smallest length-class in our analysis (100–110 mm). Bias declined but remained high even for adult length-classes (≥200 mm). The pattern of bias across length-classes was variable across years. The percentage of unadjusted counts that were below the lower 95% confidence interval from our adjusted length-frequency estimates were 95, 89, 84, 78, 81, and 92% from 2005 to 2010, respectively. Length-frequency distributions are widely used in fisheries science and management. Our simple method for correcting length-frequency estimates for imperfect detection could be widely applied when mark–recapture data are available.

Length-frequency distributions are widely used to describe fish population structure and in selecting harvest regulations (Gulland and Rosenberg 1992; Hilborn and Walters 1992; Neumann and Allen 2007). However, the size structure of a sample may not accurately represent population size structure because of bias related to gear configuration and the timing and location of sampling (Beamesderfer and Rieman 1988). For instance, gill nets and electrofishing are known to be highly size selective for many species (Dolan and Miranda 2003; Finstad and Berg 2004; Scharf et al. 2009). Clearly, the accurate

estimation of population size structure requires an unbiased sample of all size-classes.

Standardized sampling may reduce the influence of biases associated with sampling (Bonar and Hubert 2002; Miranda and Dolan 2003; Bonar et al. 2009). However, while standardization of gear, sampling effort, and other factors affecting catch may facilitate comparison among studies, it does not directly address biases associated with environmental variation or the sampling method. For instance, in studies involving electrofishing in lotic systems, variation in river discharge likely has a substantial effect on capture rates due to its relation to turbidity and water conductivity (Speas et al. 2004; Martinez and Kolz 2013). Outfitting electrofishing boats with identical electrofishing equipment would allow for a more reliable comparison among areas sampled but would not address any size-selective sampling bias associated with the electrofishing gear itself. Gear-specific size bias could be addressed empirically by sampling populations with known size structure (Bodine and Shoup 2010); however, in most field settings it will be necessary to estimate capture and recapture probabilities using mark–recapture data. Estimating detection probabilities provides a robust method to evaluate the factors affecting catch rates and allows correction of the measureable bias caused by not only the gear but also environmental variation associated with the timing and location of sampling. Adjusting for these biases provides length-frequency estimates that better represent true population size structure.

While it is well established that heterogeneity in capture probabilities among sampled individuals will lead to underestimates of population abundance (White et al. 1982; Huggins 1989, 1991; Borchers et al. 2002; Williams et al. 2002), we could find only two references that corrected for this bias in length-frequency distributions (Willis et al. 1985; Beamesderfer and Rieman 1988). An informal literature search (Web of Science) using the key words length, frequency, distribution, and fish resulted in 782 matches. We reviewed about 10% of these studies, and all inferences in each study were based on uncorrected length-frequency distributions. Without correcting for size selectivity, a source of heterogeneity in detection probabilities, estimates of length frequency (size structure) will be biased (Willis et al. 1985; Beamesderfer and Rieman 1988).

We describe a method for adjusting length-frequency distributions when capture probabilities are a function of fish length and other effects using electrofishing data from a Smallmouth Bass *Micropterus dolomieu* removal study in the upper Colorado River basin. A primary interest of basin managers was the effect of removal on the size structure of the Smallmouth Bass population over time. To evaluate these effects, we developed a method to correct length-frequency distributions for temporal, behavioral, and size-related heterogeneity in capture and recapture probabilities. We were motivated by research suggesting that electrofishing is size selective and by the wide use of electrofishing to sample freshwater fish populations in North America (Dolan and Miranda 2003; Snyder 2003; Bonar et al. 2009).

METHODS

Smallmouth Bass are a widely distributed piscivore and popular sport fish in North America. In the Yampa River of western Colorado, Smallmouth Bass are an invasive, nonnative predator that threatens the native fish assemblage (Hawkins et al. 2009). Since 2004, removal of Smallmouth Bass has been a priority on the Yampa River, including at our study site in Little Yampa Canyon, a 38.6-km (24-mi) reach located 160.9 river kilometers (100 mi) upstream of the confluence of the Green and Yampa rivers. For our analyses, we focused on boat electrofishing mark–recapture and removal data collected in this reach from 2005 to 2010.

Electrofishing gear and sampling protocols used in our study were consistent among all years and followed the recommendations of Guy et al. (2009). Electrofishing gear was deployed in two aluminum johnboats (5 m × 2.4 m) equipped with 95- or 115-hp outboard jet motors. Electrodes consisted of paired, half-submerged, 22.9-cm-diameter, stainless-steel spherical anodes suspended from the bow on fiberglass poles. The boat hull served as a cathode and was cleaned periodically to remove oxidation. One boat used a Smith-Root GPP 5.0 control box with integral generator. Anodes were extended 3.3 m from the bow and spaced 2.3 m apart. The other boat used a Coffelt VVP-15 or a Smith-Root VVP-15b control box with a single-phase, 240-V, 5,000-W generator. Anodes were extended 3.6 m from the bow and spaced 2.4 m apart. The GPP 5.0 control unit was set for pulsed DC, high range, 60 pulses per second, and duty cycle was adjusted between 20% and 50% of range. The VVP-15 or VVP-15b control boxes were set for pulsed DC, 600 V, 40% pulse width, 60 pulses per second, and current was adjusted between 4 and 7 amps. The GPP duty cycle and VVP amperage were adjusted depending on fish response with the goal of eliciting forced swimming towards the anode. Duration of effort was obtained from a timer on each electrofishing unit.

Boat electrofishing occurred from April through mid-July, starting within a week after water temperatures exceeded 10°C and ending after discharge declined below 28.3 cubic meters per second (U.S. Geological Survey, Yampa River gauge #09251000), at which point boat navigation was considered unsafe. The 38.6-km study site was divided into 48 0.8-km sections. We electrofished 9.6 km of river (both shorelines) each day during daylight hours. Each complete sweep (38.6 km) of the study site is referred to as a pass. Passes are equivalent to sampling occasions in the capture–mark–recapture analysis. The number of passes increased over the study from 4 to 11, reflecting increased priority in Smallmouth Bass removal. An interval of 0–11 d elapsed between passes.

Boat operators were trained for at least 2 years in river navigation. One netter was deployed within each electrofishing boat and was sufficient to capture all fish. Each electrofishing boat

was positioned near shore and moved in a downstream direction parallel to the shoreline at a speed similar to the current, except in high velocity areas with exposed boulders, where the boat was positioned at a slight angle to the shoreline facing upstream with the motor used to maintain position while moving backwards downstream. A third boat was used to process fish. Captured fish were placed in a live well with fresh oxygenated water and processed at the downstream end of each section. Fish length was measured to the nearest millimeter of total length (length; Neumann et al. 2012). Fish were marked and released alive on one or more marking passes each year with a uniquely numbered, model FD–94, anchor tag (Floy Tag and Manufacturing, Seattle, Washington). On nonmarking passes (all other passes), marked and unmarked Smallmouth Bass were removed from the river and either euthanized or translocated to off-channel areas (Hawkins et al. 2009). The only exception was in 2005 when Little Yampa Canyon was used to evaluate the effects of Smallmouth Bass removal on native fish populations in this reach. Little Yampa Canyon was split into a nonremoval (lower 19.3 km) and removal reach (upper 19.3 km), and all Smallmouth Bass caught on nonmarking passes were returned to the river in the nonremoval reach and euthanized or translocated to off-channel areas in the removal reach.

We used R statistical computing environment, the R package RMark, and Program MARK (White and Burnham 1999; White et al. 2001; Laake and Rexstad 2011; R Development Core Team 2011) to fit the Little Yampa Canyon dataset to the Huggins closed population, capture–mark–recapture model (Huggins 1989, 1991). We assumed demographic and geographic closure among passes within a year. Demographic closure (no births or deaths) was not an issue because water temperatures preclude Smallmouth Bass growth and reproduction this time of year, and natural mortality was minimal (e.g., very little fishing pressure) over our sampling periods. Tag recoveries in reaches directly above and below Little Yampa Canyon rarely occurred during sampling (Hawkins et al. 2009), evidence that geographic closure was also closely met. Integrating hundreds of groups, such as a group for each length bin in our analysis (250 groups; more below), was accommodated using RMark (Laake and Rexstad 2011), which is an R package (R Development Core Team 2011) that combines the model fitting and estimation features of Program MARK (RMark calls the optimization component of Program Mark, mark.exe) with the flexible programming environment of R. We provide additional details in the Appendix, and complete details are available in Laake and Rexstad (2011).

Parameters included in the Huggins model are initial capture and recapture probabilities, p and c, respectively (Huggins 1989, 1991). Abundance (N) is conditioned out of the likelihood function specified by the model, allowing individual covariates such as length to be integrated because the likelihood only includes individuals captured at least one time. Estimates of abundance are derived from the estimates of the capture probabilities ($\hat{p}$) using a form of the Horvitz–Thompson estimator (Horvitz and

Thompson 1952) proposed by Huggins (1989, 1991):

$$\hat{N} = \sum_{i=1}^{m_{t+1}} 1/\hat{p}_i^*,$$

where m_{t+1} is the number of unique individuals captured during sampling and $\hat{p}_i^*$ is an estimate of the probability of detecting the ith individual over all occasions. In a study with three sampling occasions, such as three electrofishing passes, the probability of detecting the ith individual is

$$\hat{p}_i^* = 1 - [(1 - \hat{p}_1)(1 - \hat{p}_2)(1 - \hat{p}_3)],$$

where $\hat{p}_1$, $\hat{p}_2$, and $\hat{p}_3$ are detection probabilities on passes (occasions) 1–3, respectively. The Huggins estimator is a summation of $1/\hat{p}_i^*$ that is the contribution to $\hat{N}$ made by each of the m_{t+1} individuals in the sample.

To partition the abundance estimate ($\hat{N}$) into length frequencies adjusted for imperfect detection ($\hat{N}_{jk}$), the $1/\hat{p}_i^*$ term is solved for each fish and then partitioned and summed by the jth length bin and kth year,

$$\hat{N}_{jk} = \sum_{i=1}^{m_{t+1}} 1/\hat{p}_{ijk}^*.$$

Grouping by length bin and year was accomplished in RMark before fitting the model in Program MARK using the procedure described in the Appendix.

We included length, behavior, year, pass, year × behavior, and year × pass effects on our capture and recapture probabilities. Behavior allows initial capture probability (p) to differ from recapture probability (c) and the year × behavior interaction allows the effect to vary among years. Behavior was included in the design matrix by adding a single column and inserting 1s in rows associated with capture probabilities and 0s in rows associated with recapture probabilities (Lukacs 2005). Year, pass, and year × pass interaction effects allow capture and recapture probabilities to differ among years and electrofishing passes.

Length was integrated into our analysis as an individual covariate that varies on every pass for each fish. To accomplish this we first estimated the von Bertalanffy growth coefficients k and L_∞ using a recursive finite difference equation of the von Bertalanffy growth model (White and Brisbin 1980), $L_{i+1}^g = (g_{i+1} - g_i)k(L_\infty - L_i^g) + L_i^g$, where L_i^g is the length on growth day i and g_i is the growth day; $g_{i+1} - g_i$ is always equal to 1. In this analysis, we only used Smallmouth Bass that were marked and subsequently recaptured and had an initial capture length and a recapture length ($n = 992$; length range based on initial capture length was 117–462 mm). We defined a growth day as any day when water temperatures were $\geq 20°$C. Smallmouth Bass are most active (feeding) when water temperatures are in the 20–28°C range and are inactive in water

below 10–15°C (Wallus 2008). Growth rates are very slow between inactive and preferred temperature ranges (Wallus 2008). Water temperature data were acquired from the U.S. Geological Survey gauge #09251000 just downstream of Little Yampa Canyon. The von Bertalanffy model was implemented recursively for each growth day between capture and recapture for each fish. For example, for a fish that experienced 10 growth days between capture and recapture model fitting started with this fish's initial capture length and initial estimates for k and L_∞. These starting parameters were then used to predict the fish's length on growth day 1 (L_1^g). The predicted length on growth day 1 was then used to predict length on growth day 2 (L_2^g). This recursive process was repeated until length on day 10 (recapture length) was predicted. The relationship between the predicted length and the actual recapture length was modeled using the NLIN procedure in SAS Version 9.2 (SAS 2008; White and Brisbin 1980) and k and L_∞ were fit to minimize the nonlinear least squares based on the Gauss-Newton algorithm.

Using the von Bertalanffy growth coefficients, we estimated the total length of all fish on all passes preceding and following initial capture with the equation $L_{i+1}^p, L_{i-1}^p = (n)\hat{k}(\widehat{L_\infty} - L_i^p) + L_i^p$, where $\hat{k}$ and $\widehat{L_\infty}$ are estimates of the von Bertalanffy growth coefficients, L_i^p is length on pass i, and n is the number of growth days (defined above) between L_i^p and subsequent pass L_{i+1}^p or L_i^p and previous pass L_{i-1}^p. If a fish was captured on the first pass its length was predicted for all subsequent passes (L_{i+1}^p), if it was captured on the last pass its length was predicted for all previous passes (L_{i-1}^p), and if it was caught on an intermediate pass its length was predicted in both directions.

We assessed the biological and statistical significance of length, behavior, year, pass, year × behavior, and year × pass effects on our capture and recapture probabilities using Akaike information criterion adjusted for small sample size (AIC_c), AIC_c weights, and odds ratios (Neter et al. 1996; Burnham and Anderson 2002). We adopted the rules of thumb proposed by Burnham and Anderson (2002, page 70) for determining empirical support for each model in our set: all models within 2 AIC_c units were considered top models with substantial empirical support, those within 4–7 AIC_c units had considerably less empirical support, and those above 10 AIC_c units had essentially none. We estimated percent relative bias using

$$\widehat{bias} = \frac{C - \hat{A}}{\hat{A}} \times 100$$

to quantify the differences between our unadjusted length-frequency counts (C) and adjusted counts ($\hat{A}$) from our mark–recapture analysis. We also calculated the proportion of the unadjusted counts that were less than the lower 95% confidence interval of our adjusted counts. We calculated proportional size distribution using the established stock length for Smallmouth Bass of 180 mm and 280 mm as the quality length (Gabelhouse et al. 1984; Guy et al. 2007; Neumann et al. 2012). We used the formula from above to calculate percent relative bias using unadjusted proportional size distribution (C) and adjusted proportional size distribution ($\hat{A}$).

RESULTS

Despite consistent electrofishing effort among passes and years (Table 1), the numbers of fish captured by pass varied (Table 2). Environmental and sampling effects responsible for variability in the number of fish captured on each pass is accounted for by pass, year, and pass × year factors described below. Estimates of the von Bertalanffy growth coefficient k and the asymptotic length L_∞ used to estimate fish total length before and after initial capture were 0.0038 (95% confidence limits = 0.0032, 0.0043) and 458.8 (95% confidence limits = 425, 492.6), respectively. The predicted and actual recapture lengths were highly correlated (linear regression: $r^2 = 0.998$, slope = 1.003).

The capture–mark–recapture model including all main effects and interactions acquired 100% of the AIC_c weight. The length effect was significant ($\beta = 0.0095$; 95% confidence limits = 0.0088, 0.0101; logit scale). Based on odds ratios of the length effect, electrofishing crews were 2.6 times more likely to capture or recapture a 200-mm fish than a 100-mm fish and 6.7 times more likely to capture or recapture a 300-mm fish than a 100-mm fish. The biological significance of the other main effects and interactions in our top model can be visualized

TABLE 1. Hours of electrofishing effort by pass and year from Little Yampa Canyon, Yampa River, Colorado, during 2005–2010.

Year						Pass						Total
	1	2	3	4	5	6	7	8	9	10	11	
2005	46.7	36.8	33.0	32.1								148.6
2006	29.1	32.4	37.4	30.3	27.8	28.2	25.8					210.8
2007	25.3	37.6	24.7	32.4	11.4	28.1	15.5	17.7				192.6
2008	36.2	46.8	48.3	35.3	38	38.3	52.2					295.1
2009	19.2	23.3	21.1	27.9	32.9	34.4	32.4	28.6	28.0	22.8	30.2	300.8
2010	29.1	22.5	30.6	29.7	36.5	31.9	36.1	28.8	9.2	30.5		284.5

TABLE 2. Number of Smallmouth Bass ≥100 mm captured by pass and year from Little Yampa Canyon, Yampa River, Colorado, during 2005–2010.

Year	Pass											Total captured	Total marked
	1	2	3	4	5	6	7	8	9	10	11		
2005	407	575	494	564								2,040	1,136
2006	270	329	618	159	192	352	145					2,065	548
2007	145	335	230	192	101	303	215	114				1,635	133
2008	251	266	466	474	241	304	756					2,758	250
2009	26	38	19	220	420	448	320	154	162	145	527	2,479	220
2010	103	12	85	196	466	380	180	256	59	420		2,157	292

by comparing plots of capture (p) and recapture (c) probabilities across years (Figure 1). For example, the substantial difference in capture and recapture probabilities on the same pass within a year is a function of the behavior effect (β = 0.55; 95% confidence limits = 0.1660, 0.9406; logit scale). Changes in detection probability across passes (e.g., 2008) demonstrate the biological significance of variation in detection probability that is a function of pass. Comparing plots across years demonstrates the biological significance of variation in detection probability that is a function of year.

Uncorrected length frequencies of fish removed from Little Yampa Canyon were negatively biased in every year, particularly for smaller length-classes (Figure 2). Estimates of percent relative bias suggested that unadjusted length-frequency counts were biased by as much as –88% relative to our mark–recapture estimates for the smallest length-class (100–110 mm; Figure 3). Relative bias declined but remained high even for adult length-classes (≥200 mm); bias was zero for only the largest length-classes considered, those longer than about 400 mm. The pattern of percent bias across length bins was variable across years. The lowest bias between unadjusted and adjusted counts occurred in 2008 and the highest in 2005 (Figure 3). The percentage of unadjusted counts that were below the lower 95% confidence interval from our adjusted length-frequency estimates were 95, 89, 84, 78, 81, and 92% from 2005 to 2010, respectively. The corrected length frequencies yielded a higher proportional size distribution in every year and the percent relative bias varied from 12% to 35% (Figure 2).

DISCUSSION

We demonstrated that length frequencies are sensitive to variation in detection probability caused by variation in electrofishing efficiency. Efficiency in our study was influenced by fish length, annual variation (year), temporal variation within a year (pass), whether a fish had been captured previously (behavior), and interactions (year × behavior and year × pass). Uncorrected length frequencies underestimated size structure and the bias was most pronounced for smaller size-classes.

Our analyses indicate that detection probability is an important consideration when assessing fish length frequencies; not adjusting for detection probability could contribute to misinterpretation of fisheries data. For example, adjusted length frequencies in 2006 clearly indicate substantial recruitment of 100–150-mm length-classes, an insight that would go undetected without adjusting for detection probability (Figure 2). Although Smallmouth Bass in the Yampa River are an undesirable invasive predator and not managed as a fishery, it is informative to use our length-frequency data to calculate a proportional size distribution. The corrected length frequencies yielded a higher proportional size distribution in every year, and the percent relative bias varied from 12% to 35% (Figure 2). Clearly, using length-frequency data not adjusted for imperfect detection can result in erroneous conclusions regarding population structure and dynamics with implications for management.

One suggestion to reduce the influence of sampling biases is to standardize gear configuration, sampling effort, and timing of sampling (Bonar et al. 2009), and recent research has made substantial contributions to standardizing electrofishing equipment to reduce bias and facilitate comparisons among studies (Miranda 2005, 2009; Martinez and Kolz 2009). We agree that standardization will reduce bias associated with sampling; however, it will not eliminate it. For instance, even though our sampling was standardized and consistent over time, we found substantial variation in capture probabilities among years and passes. Although we did not analyze the specific causes of interannual and among-pass variation, these are likely due to environmental differences, such as river discharge. Changes in discharge are usually associated with changes in turbidity, which would influence water conductivity and possibly the ability to see and net fish. Despite attempts to standardize gear and other sampling protocols such as timing of sampling, variation in capture efficiency will likely remain a source of bias in length frequencies with significant implications for managers.

Our focus on electrofishing was motivated by the ubiquity of this sampling technique in North America and studies that suggest electrofishing detection probabilities are a function of fish length (Dolan and Miranda 2003; Snyder 2003; Bonar et al. 2009; Scharf et al. 2009). However, we suspect that many other

gear types, including nets of varying types and mesh sizes, are also susceptible to variation in detection probability caused by variation in fish length (Willis et al. 1985; Beamesderfer and Rieman 1988; Finstad and Berg 2004; Colombo et al. 2008). Without correction, these other gear types would likely produce biased length-frequency distributions, with the direction and magnitude of the bias dependent on the gear, species, and other environmental factors associated with gear efficiency.

Length-frequency distributions are widely used in fisheries science to describe population structure and to define legal harvest quotas and sizes (Hilborn and Walters 1992; Neumann and Allen 2007; Quist et al. 2009; Annala and Eayrs 2010; Haddon 2011). Given the wide use of length-frequency distributions in fisheries science, we suggest that more mark–recapture studies be conducted to quantitatively assess bias associated with factors influencing capture and recapture probability. Our study
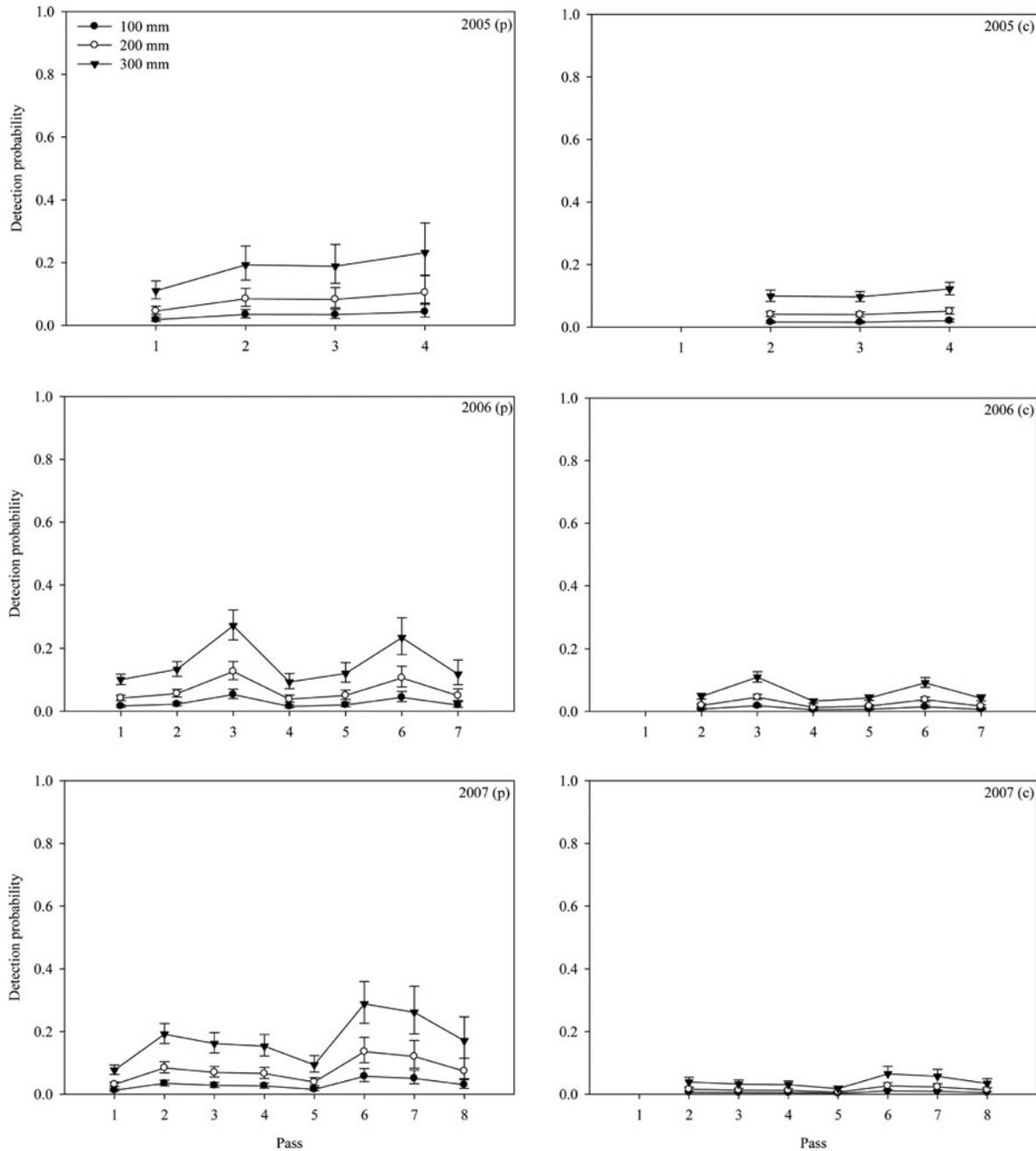

FIGURE 1.   Estimates of Smallmouth Bass capture (*p*) and recapture (*c*) probabilities as a function of year, pass, behavior, length, year × pass, and year × behavior interactions from Little Yampa Canyon, Yampa River, Colorado, in 2005–2010. Error bars are 95% confidence intervals.
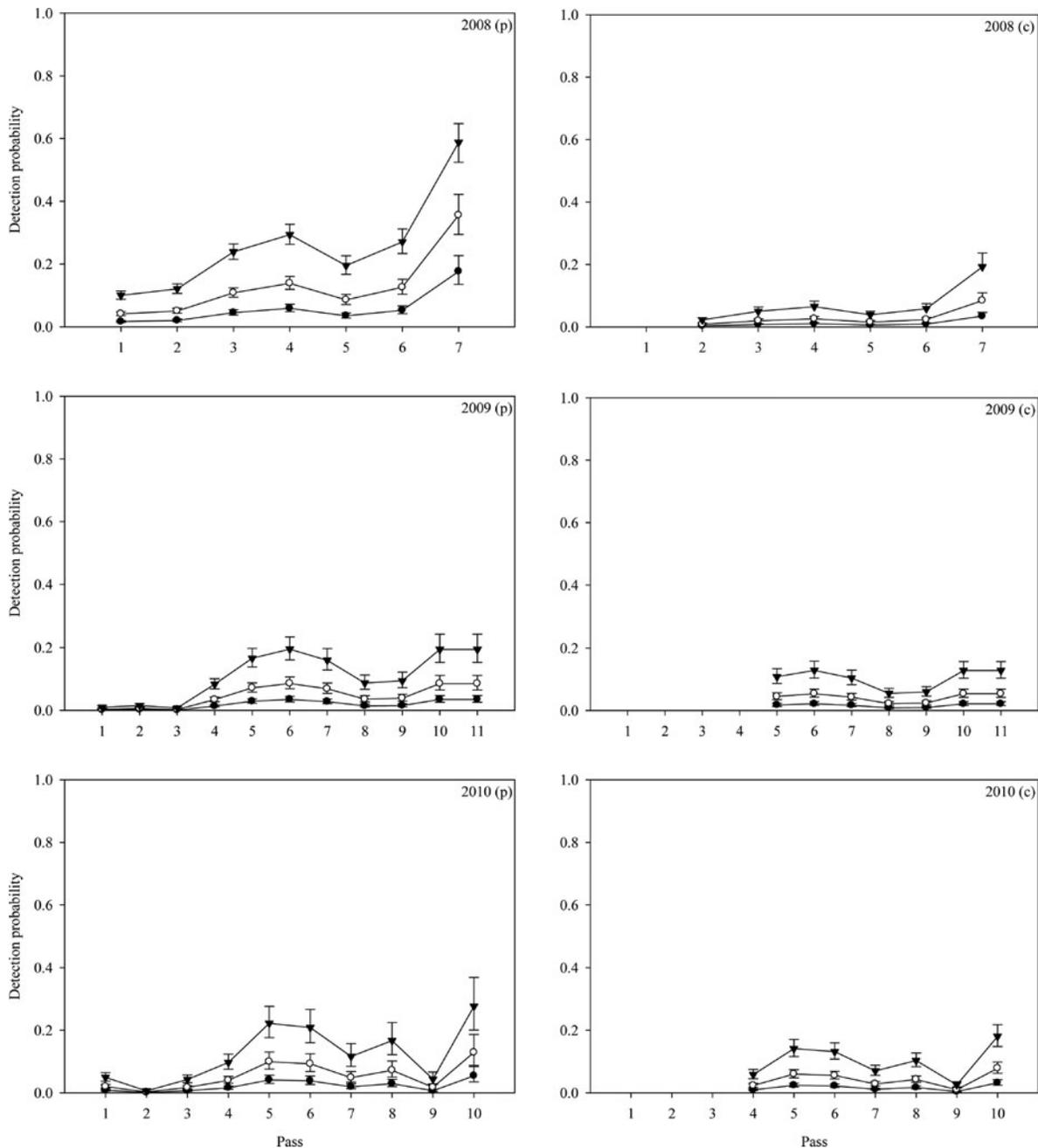
FIGURE 1. Continued.

suggests that dynamic ecosystems, such as the Yampa River, that have substantial changes in flow, turbidity, and temperature among sampling events and years will have significant bias in length frequencies associated with these environmental factors. In our study, variation in detection probabilities occurred despite significant efforts to standardize gear configuration and train sampling crews. We suggest caution when inferring population dynamics from length-frequency data collected in these situations and ideally mark–recapture studies should be conducted

to quantitatively assess bias associated with factors influencing capture and recapture probabilities. In less temporally dynamic ecosystems, length-frequency bias may be less important. For instance, if environmental variation is temporally predictable, then sampling consistently during the same season may be sufficient to make annual length-frequency comparisons possible. However, more quantitative mark–recapture studies will need to be done to assess this approach or to establish if a simpler correction may be available in these situations. We feel that
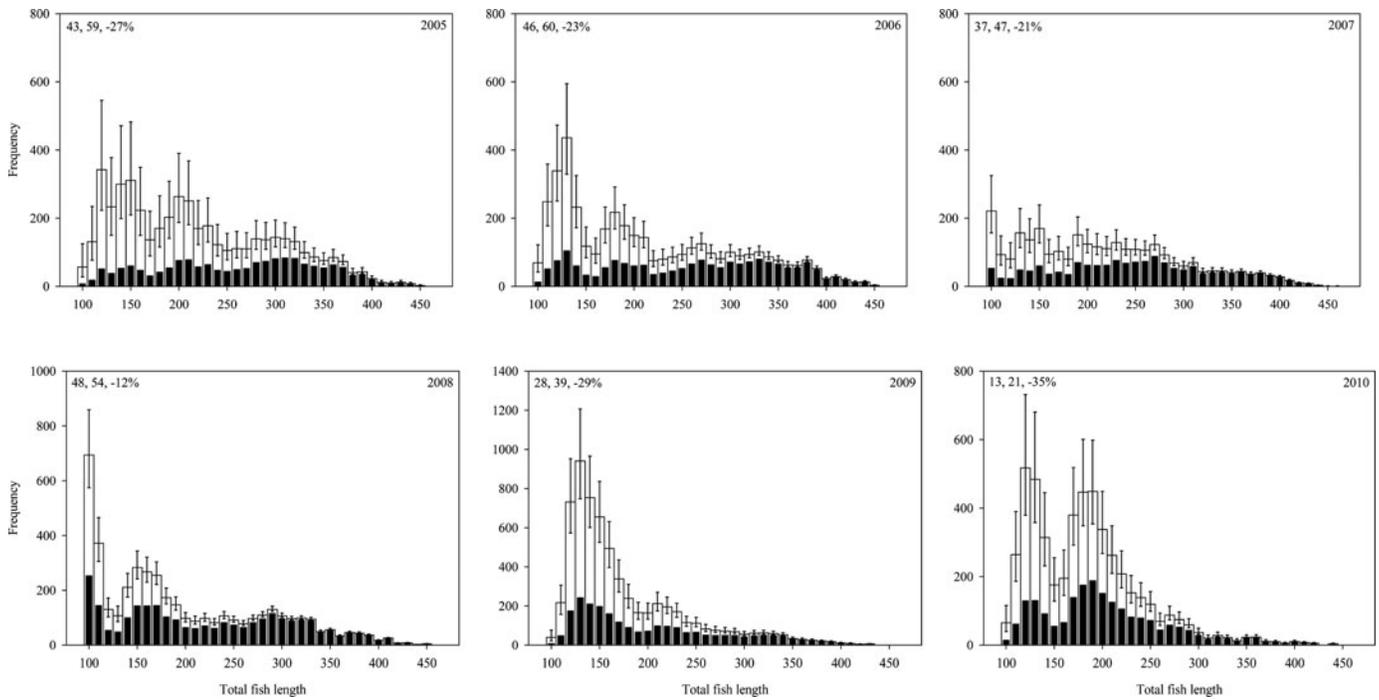
FIGURE 2.   Length-frequency distributions of Smallmouth Bass corrected for length, behavior, year, pass, year × behavior, and year × pass effects on capture and recapture probabilities (white bars) and uncorrected length frequencies (black bars) from an electrofishing mark–recapture and removal study in Little Yampa Canyon, Yampa River, Colorado, during 2005–2010. Error bars are asymmetric, lognormal, 95% confidence intervals. Note that the frequency scale is different in 2008 and 2009 relative to all other years. Also provided (top left corner, each plot) is the proportional size distribution (stock length, 180 mm; quality length, 280 mm) for the unadjusted counts, adjusted counts, and the percent relative bias between unadjusted and adjusted counts.
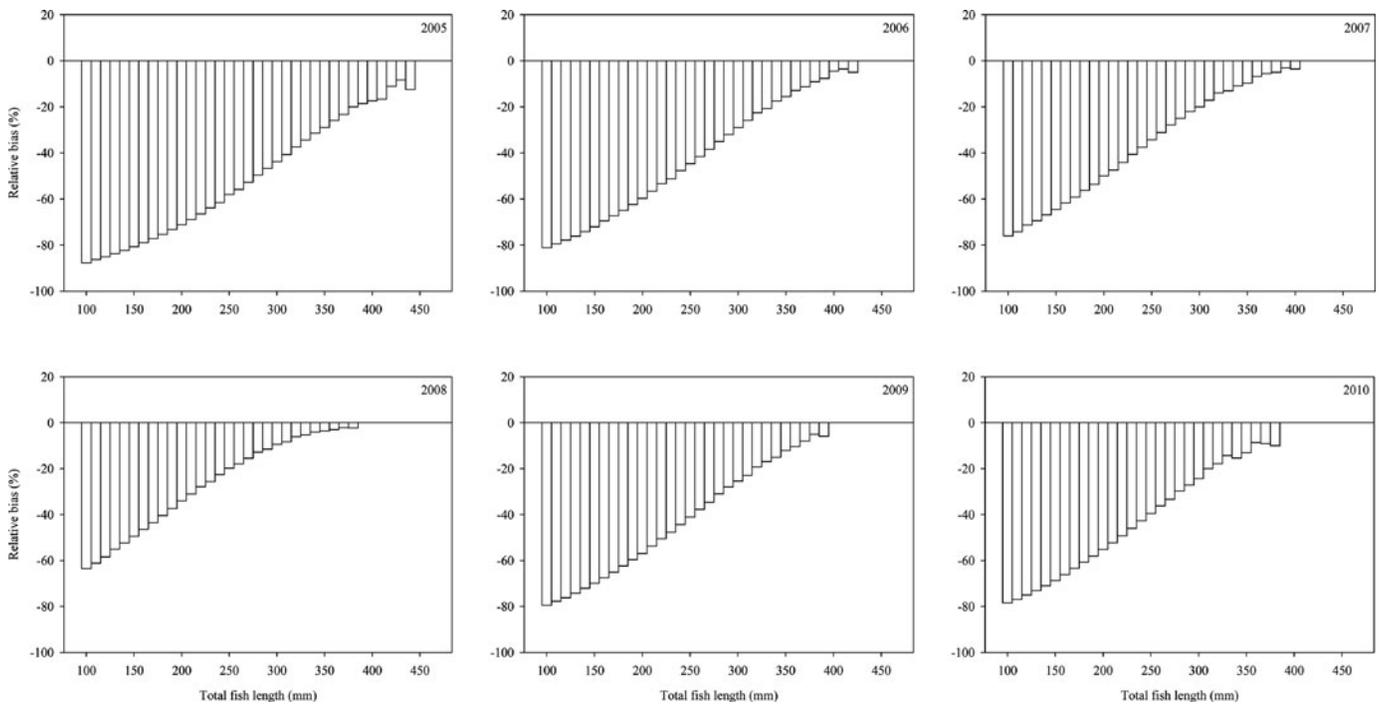

FIGURE 3.   Estimates of percent relative bias of the unadjusted count relative to the estimated length-frequency (adjusted count) from our mark–recapture analysis; unadjusted counts were always less than or equal to the adjusted counts. For example, the unadjusted count of 100–110-mm Smallmouth Bass from 2005 underestimated our adjusted count by 88%.

our analytical approach for correcting bias in length frequencies could be widely applied when mark–recapture data are available and could answer fundamental questions regarding population dynamics of size-structured populations.

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APPENDIX: RMARK ADDITIONAL DETAILS

Initially, we converted an encounter history input file we developed for the Program MARK interface into an RMark dataframe using the following:

LYC=convert.inp("C:/path/mark_file_name.inp,"group.df=data. frame(stage=rep(c("SA,""A"),6),syear=c(rrep("2005",2), rep("2006",2),rep("2007",2),rep("2008",2),rep("2009",2), rep("2010",2))),covariates=c("L1","L2","L3","L4","L5", "L6","L7","L8","L9","L10","L11","Length_Bin"),use. comments=FALSE).

The dataframe name is LYC, referring to Little Yampa Canyon. Within this dataframe are the group and covariate information and data path. At this point we have identified groups as unique combinations of stage (SA = subadult; A = adult) and sample year (syear), 2005–2011. Our list of covariates is fish length on passes 1–11 and 10-mm length bin. The "rep" refers to repeat and "c" to concatenate; these are R functions. There were 12 numeric group columns in our MARK input file, 2 columns for each year starting with 2005. Within a pair of year columns, the first column identifies the frequency of subadults and the second adults. RMark collapses the group columns down to a single group column and populates each cell with the appropriate group, such as SA2005 (i.e., subadult in 2005).

Our LYC dataframe fulfills the data argument in process.data. Other arguments in this function include the data type ("huggins"), time intervals between sampling occasions, first year of the study, and number of mixtures. In the group argument below, we have identified that we want to group by sample year and stage:

LYC.huggins=process.data(LYC,model="Huggins,"begin. time=2005,mixtures=1,time.intervals=c(1,1,1,1,1,1,1,1, 1,1), groups=c("syear,""stage")).

To group by 10-mm length bins and sample year we changed the group argument to the following: groups=c("syear," "Length_Bin"). We named our processed data LYC.huggins to make explicit the source of the data and data type.

Next, we specified an RMark function called make. design.data: LYC.ddl=make.design.data(LYC.huggins).

The data argument is fulfilled by LYC.huggins. Our name for these design data, LYC.ddl, follows an RMark naming convention—ddl refers to "design data list" (Laake and Rexstad 2011). Next we specified parameters that we wanted to fix to zero (not shown), identified the PIM structure that we needed to build our model (not shown), and stored a vector of values called "initial" to start our optimization (not shown; see Laake and Rexstad 2011 for more details). Lastly, we incorporated all of these steps into the function called mark:

LYC.huggins.M.full=mark(LYC.huggins,LYC.ddl, model= "full," model.parameters=list(p=p.full.fix.shared),output= FALSE, initial=initial),

where LYC.huggins.M.full is the name we've given to this RMark object. Our name integrates the source of the design data (LYC.huggins), "M" refers to model, and "full" refers to a model with all main effects and interactions previously described. Our process data, LYC.huggins, and our design data, LYC.ddl, fulfill data arguments in the mark function. The PIM structure is specified by model.parameters. In this case, the full effects model with fixed parameters and many effects shared across p and c (see Laake and Rexstad 2011 for more details). Output prints mark.exe results to the R console unless it is set to false, and initial is a vector of values used to start the optimization in mark.exe. Estimates of abundances and frequencies output by mark.exe are provided with asymmetric, lognormal, 95% confidence intervals. These incorporate m_{t+1} to avoid reporting a lower interval that is less than the number of individuals sampled.

APPENDIX REFERENCES

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