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[Article]

Effects of Fish Size, Habitat, Flow, and Density on Capture Probabilities of Age-0 Rainbow Trout Estimated from Electrofishing at Discrete Sites in a Large River

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Abstract.—We estimated size-specific capture probabilities of age-0 rainbow trout *Oncorhynchus mykiss* in the Lee's Ferry Reach of the Colorado River, Arizona, by backpack and boat electrofishing at discrete shoreline sites using both depletion and mark–recapture experiments. Our objectives were to evaluate the feasibility of estimating capture probability for juvenile fish in larger rivers; to determine how it is influenced by fish size, habitat, flow, density, and recovery period; and to test population closure assumptions. There was no mortality among the 351 rainbow trout that were captured by electrofishing, marked, and held for 24 h. Of a total of 2,966 fish that were marked and released, only 0.61% were captured outside of mark–recapture sites, and total emigration from mark–recapture sites was 2.2–2.6%. These data strongly suggest that populations within discrete sites can be treated as effectively closed for the 24-h period between marking and recapture. Eighty percent of capture probability estimates from 66 depletion experiments and 42 mark–recapture experiments ranged from 0.28 to 0.75 and from 0.17 to 0.45, respectively, and the average coefficient of variation of estimates was 0.26. There was strong support for a fish size–capture probability relationship that accounted for the differences in vulnerability across habitat types. Smaller fish were less vulnerable in high-angle shorelines that were sampled by boat electrofishing. There was little support for capture probability models that accounted for within-day and across-month variation in flow. The effects of fish density on capture probability were challenging to discern, variable among habitat types and estimation methodologies, and confounded with the effect of fish size. As capture probability estimates were generally precise and the closure assumption was met, our results demonstrate that electrofishing-based mark–recapture experiments at discrete sites can be used to estimate the abundance of juvenile fish in large rivers.

Catch information has a variety of uses in the study of animal populations, but all require an understanding of the dynamics of capture probability, which is the proportion of a population that is captured per sampling event (Williams et al. 2002). For example, in commercial or recreational fisheries, changes in catch per effort over time can be used to assess trends in abundance under the assumption that capture probability has remained stable or, alternatively, that temporal changes in capture probability can be estimated (Hilborn and Walters 1992). In scientific surveys of stream-dwelling fishes, differences in catch rates among habitat types can be used to evaluate the relative importance of those habitats, but only if the capture probabilities in these habitats are known. Studies conducted over a period in which fish are growing and undergoing ontogenetic habitat shifts must account for the effects of both changes in fish size and habitat use on capture probability. Efforts targeted at improving the status of freshwater fish populations, such as increasing minimum stream flows in regulated rivers, are sometimes assessed by comparing catch rates before and after flow changes. In this situation, it is important to understand how persistent environmen-

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tal changes, such as flow, potentially alter capture probability. A common assumption required in all such studies is that catch rates are proportional to abundance; in other words, that capture probability is independent of density.

Electrofishing is a commonly used means of sampling stream-dwelling juvenile salmonids and other fishes. A variety of studies have investigated the effects of electrofishing on movement (Dunham et al. 2002; Young and Schmetterling 2004) and behavior (Cross and Stott 1975; Mesa and Schreck 1989; Ainslie et al. 1998), and how capture probability is influenced by habitat and environmental variables (Bayley and Austen 2002; Peterson et al. 2004; Rosenberger and Dunham 2005), fish size (Borgstrom and Skaala 1993; Anderson 1995), and density (Bayley and Austen 2002). The vast majority of studies have been conducted in small streams and lakes or in very small artificial systems. Very few have been undertaken in medium- to large-sized rivers. Speas et al. (2004) found that capture probability for adult rainbow *Oncorhynchus mykiss* and brown trout *Salmo trutta* in the Colorado River (mean annual discharge [MAD] = 385 m^3/s) varied with turbidity, and was density-independent and density-dependent for rainbow trout and brown trout, respectively. Mitro and Zale (2002) used mark–recapture to estimate capture probability for age-0 rainbow trout in a tributary of the Snake River (MAD = 24 m^3/s). They found that capture probabilities at discrete sites tended to be low (average = 0.17), and that sites could be treated as effectively closed because emigration rates of marked fish were relatively low (16%). To our knowledge, there have been no attempts to estimate capture probabilities at discrete sites for juvenile fish in large rivers using depletion or mark–recapture experiments, or other methods. This represents a significant limitation in our ability to estimate the abundance, distribution, growth, and survival of juvenile fish in these environments, which is critical for understanding effects of habitat enhancement and other management efforts.

The objective of this paper is to evaluate the feasibility of estimating capture probabilities for juvenile fish populations in larger rivers. We define capture probability as the proportion of a population within a discrete shoreline site that is removed by a single-pass of electrofishing effort. The assumption that populations within sites can be treated as closed is evaluated based on the recovery rates of marked fish outside of mark–recapture sites and by 24-h holding experiments to determine the potential mortality of fish between the release and recovery periods. We compare capture probabilities estimated by depletion and mark–recapture experiments, and examine how capture probabilities vary with fish size, habitat, flow, recovery period, and density. The results from this investigation should be of interest to researchers wishing to study the population dynamics of small or juvenile fish in large river environments.

Methods

Study area.—This study was conducted in the Lee's Ferry reach of the Colorado River, Arizona, which begins at Glen Canyon Dam below Lake Powell and extends 26 km downstream to the confluence with the Paria River (latitude = 36.86638; longitude = −111.58638). The average flow during months when the study was conducted in 2006 (July–November) and 2007 (June–November) was 325 and 339 m^3/s, respectively (U.S. Geological Survey [USGS] gauge 09380000). Although located in a canyon, the reach is broad, shallow, and low gradient. The average wetted width, depth, and gradient at 325 m^3/s are 144 m, 5.2 m, and 0.25 m/km, respectively (Randle and Pemberton 1987). There are no significant tributary inputs to the reach, and water quality is determined by the hypolimnetic release from Glen Canyon Dam. The annual range of main-stem water temperatures recorded at the downstream end of the reach since 2003 has ranged from 9–15°C (Voichick and Wright 2007), and Secchi depths have consistently ranged from 6 to 7 m (Vernieu et al. 2005). The fish fauna in the Lee's Ferry reach is almost exclusively comprised of a large, self-sustaining population of nonnative rainbow trout (McKinney et al. 2001).

Flow from Glen Canyon Dam normally fluctuates on a diel cycle that is driven by power demand but controlled through regulation of the maximum daily flow range (141–227 m^3/s), minimum (141 m^3/s) and maximum (708 m^3/s) flows, and maximum downramp (42 $m^3/s \cdot h$) and upramp (113 $m^3/s \cdot h$) rates. There is little variation in flow during the low- and high-flow periods within a day. Flow was very similar within months across years during the study period (Table 1), being relatively high with large daily flow variation during summer months (June–August), and low with less daily variation during fall (September–November).

Field methods.—Depletion and mark–recapture methods were used to estimate capture probability and population size for age-0 rainbow trout at discrete sites within the Lee's Ferry reach. Both these methods rely on the assumption that a population within a site can be treated as effectively closed; in other words, that the number of fish that migrate from or into the site, or that die over the period when the site is sampled, is negligible. Shoreline habitat in the reach has been classified into the following five strata based on low-level aerial photographs: cobble bars, vegetated sand

TABLE 1.—Average monthly discharge and average daily minimum and maximum flows (m^3/s) in the Lee's Ferry reach during the study months in 2006 and 2007. The daily range is the difference between the daily minimum and the daily maximum.

Year	Month	Average	Daily minimum	Daily maximum	Daily range
2006	Jun	381	253	476	223
	Jul	381	269	491	223
	Aug	381	269	493	224
	Sep	253	173	312	138
	Nov	285	197	368	171
2007	Jun	381	253	475	222
	Jul	370	255	475	220
	Aug	370	255	478	223
	Sep	287	182	351	169
	Nov	288	202	368	167

bars, debris fans, talus (large angular boulders), and cliffs (Mietz 2003). In total, there are 96 shoreline habitat units summing to 56.5 km. The total shoreline length is slightly greater than twice the total length of the river because it includes both banks and the shorelines are more sinuous than the centerline of the channel. We reclassified the five original habitat strata into low- (cobble and vegetated sand bars and debris fans summing to 27.8 km of shore length) and high-angle (talus slopes summing to 21.5 km of shore length) shoreline habitat types that could be sampled by backpack and boat electrofishing, respectively. Cliff habitat was excluded because it comprises only 12% of the total shoreline length and because pilot sampling showed it was very rarely utilized by age-0 rainbow trout. The sites at which the depletion or mark–recapture experiments were conducted were randomly selected units from low- and high-angle habitat strata.

All sampling was conducted after dark between midnight and 0600 hours when sampling at the daily minimum flow and between 2100 and 2300 hours when sampling at the daily maximum flow. Electrofishing sites extended 3–4 m from shore, were not enclosed by block nets, and were fished very methodically in upstream (backpack electrofishing) or downstream (boat electrofishing) directions. The effects of daylight and flow on the distribution of age-0 rainbow trout within the immediate shoreline areas that were electrofished are explored in a companion paper (Korman and Campana 2009, this issue). Backpack and boat electrofishing were conducted by a two-person crew operating Smith-Root Type 12b and Coffelt CPS electrofishers, respectively. A single pass of electrofishing required an average of 10 s of electrofishing effort per meter of shoreline sampled. Boat electrofishing was conducted from a shallow-draw, 5.3-m aluminum boat (50-hp [1 hp = 746 W] outboard motor with power trim). The combination of boat design, highly experienced operators, and slow shoreline water velocities allowed fine control of anode position and very thorough coverage of the immediate shoreline area relative to typical boat electrofishing operations. After electrofishing, fish were anesthetized with clove oil, and fork lengths were measured to the nearest millimeter.

In 2006, 66 depletion experiments ($n = 19$ in low-angle and 47 in high-angle habitats) were conducted over four sampling trips between July and November (Tables 2, 3). Experiments were conducted at either the daily minimum ($n = 42$) or maximum ($n = 24$) flow. Each depletion experiment consisted of repeatedly removing fish from a single site over three ($n = 62$) or four ($n = 4$) passes and holding them until the experiment was complete. We allowed a 1–2-h period between passes and ensured that fishing effort (seconds shocked per meter of shoreline) was approximately constant among passes (±15%). Site lengths varied and depended on the number of fish captured on the first pass. At a minimum, sites were 30 and 50 m long in low-angle and high-angle shorelines, respectively,

TABLE 2.—Summary statistics for data collected from depletion experiments. The daily flow column denotes whether sampling was conducted at the daily minimum or maximum flow; total catch is total number of fish caught over three passes across sites; and average FL = the average fork length of fish caught on the first pass.

Habitat type	Daily flow	Sampling month	Sites sampled	Meters sampled	Total catch	Average FL (mm)
Low angle	Minimum	Jul	5	150	217	41
		Aug	6	204	188	45
	Maximum	Aug	5	221	113	51
		Sep	3	120	55	63
High angle	Minimum	Jul	8	400	384	54
		Aug	8	400	463	59
		Sep	7	377	214	67
		Nov	8	589	272	79
	Maximum	Aug	8	486	195	59
		Sep	6	323	132	71
		Nov	2	125	29	78

TABLE 3.—Summary statistics for data collected from mark–recapture experiments. Abbreviations are as follows: M = the total number of fish marked; r = the total number of marked fish recaptured; average FL = average fork length of fish caught on the first pass.

Habitat type	Recovery period	Sampling month	Sites sampled	Meters sampled	M	r	r/M	Average FL (mm)
Low angle	1 h	Aug	2	280	424	239	0.56	43
	24 h	Jul	3	218	271	31	0.11	36
		Aug	2	283	365	97	0.27	44
High angle	1 h	Jul	4	272	203	46	0.23	55
		Aug	4	247	264	94	0.36	57
		Sep	1	57	46	13	0.28	61
	24 h	Jun	5	279	58	16	0.28	90
		Jul	4	271	196	46	0.23	60
		Aug	4	265	214	63	0.29	62
		Sep	4	360	192	38	0.20	62
		Nov	9	1,324	723	227	0.31	84

but were extended up to approximately twice these distances if time permitted or if catches were low. In the rare cases in which 10 fish were not captured over the maximum distance, the site was abandoned and another random site was selected. Average site lengths in low- and high-angle habitats were 37 (range = 30–61 m) and 57 m (range = 50–116 m), respectively.

In 2007, we conducted 42 mark–recapture experiments over five sampling trips between June and November (n = 7 and 35 in low- and high-angle habitats, respectively; Table 3). On the first pass (marking pass), fish were captured by electrofishing and measured to the nearest millimeter. Live fish were put in an aerated bucket containing neutral red biological stain (2 g/15 L; Sigma-Aldrich, Ltd.) for 20 min and then transferred to aerated buckets of clear water to recover (Gaines and Martin 2004). The fork lengths of dead fish and those that were not actively swimming after processing were recorded so they could be excluded from the count of marked fish released into the site. The remaining marked fish were released one or two at a time near the shore throughout most of the length of the sample site. No fish were released within 5 m of the upstream or downstream borders of the sites. Sites were resampled by electrofishing either 1 (n = 11) or 24 h (n = 31) after fish were released. All sites were resampled at the same flow at which they were initially sampled, and sites resampled after 24 h experienced a complete diel flow cycle. Effort (seconds electrofished per meter of shoreline) during the second pass (recapture pass) was consistent with effort during the initial marking pass and during depletion experiments in 2006. The number and fork length of marked and unmarked fish that were captured on the second pass were recorded. Average site lengths in low- and high-angle habitat were 112 (range = 95–273 m) and 88 m (range = 50–247 m), respectively. Twenty-five-meter-long shoreline sections located immediately upstream and downstream of each of the mark–recapture sites were sampled at the end of the recapture pass. The number of marked fish captured in these areas was expanded by the estimated site-specific capture probabilities to determine the total number of marked fish that had emigrated between marking and recapture events.

To determine whether electrofishing, handling, and staining resulted in postrelease mortality of marked fish, we conducted two holding experiments in September 2007. A large sample of fish were captured by backpack and boat electrofishing, and measured to the nearest millimeter. One-half of all fish with fork lengths greater than 60 mm had a small portion of the upper lobe of their caudal fin removed and were held for 20 min in clear water. The other half of fish larger than 60 mm and all fish 60 mm or smaller were placed in neutral red stain for 20 min. This design allowed us to determine whether use of the neutral red stain resulted in additional mortality relative to the more traditional method of marking juvenile fish using fin clips. Fish were then put in mesh baskets (1 × 0.5 × 0.4 m) that were placed on the stream bottom in calm water. We returned to the baskets after 24 h, and counted and measured the number of stained and clipped live and dead fish.

Model structure and estimation.—Capture probability (p) and population size were estimated from depletion and mark–recapture experiments following the generalized mark–recapture and depletion models of Otis et al. (1978). Capture probability may change across passes owing to changes in effort, or because of the effects of past fishing effort on physical habitat (i.e., increasing turbidity) or fish behavior (Mesa and Schreck 1989; Peterson et al. 2004). We therefore evaluated two alternative depletion models: (1) a simpler model in which the capture probability was constant across passes (model D_1, where D refers to a depletion experiment and the subscript 1 refers to the number of capture probabilities that are estimated) and (2) a more complex model in which the capture probability varies from pass to pass (D_2). We evaluated simple and complex mark–recapture models in which capture probability was assumed either to be constant across passes (MR_1) or to vary (MR_2). Parameters for depletion and mark–recapture models were estimated by maximizing the log of the multinomial probability that depends on differences between the observed and predicted number of fish with different capture histories. This approach exactly follows Otis et al. (1978). Computations were done with AD Model Builder (ADMB) software (Otter Research 2004). Population density per 100 m of shoreline (N) was calculated by dividing the most likely estimate (MLE) of population size by the site length and multiplying by 100. The approximate asymptotic estimate of SE for the MLE of capture probability was computed from the inverse of the Hessian matrix returned by the ADMB software. The coefficient of variation (CV) for capture probability estimates, computed as the ratio of SE of the MLE to the MLE, was used to provide a standardized measure of uncertainty.

The influence of fish size on capture probability was modeled using mark–recapture data, where the size distribution of marked fish present at the start of the recapture event is known. Data from each mark–recapture experiment were aggregated into 10-mm fork length-classes. The capture probability for each length-class was predicted by means of the following model:

$$pL_j = \frac{\beta}{1 + \exp\left[\frac{-(\bar{L}_j - \mu)}{\sigma}\right]}, \qquad (1)$$

where $pL_{,j}$ is the predicted capture probability for the 10-mm size-class j (e.g., $j = 4$ for size-class 30–40 mm) and a midpoint fork length $\bar{L}_j$ (mm), β is the base capture probability (the capture probability for which size is not limiting, i.e., when the denominator = 1), and μ and σ are the mean and SD of the logistic fork length–vulnerability function that determine the length at which capture probability is 50% of the maximum and the inverse of the slope of the relationship, respectively. We fit equation (1) to data stratified by habitat type as well as aggregated across habitats. Parameters were estimated by maximizing the sum of the log likelihood of the binomial probability of the number of recaptures across all length-classes, that is,

$$r_{i,j} \sim \text{binomial}(M_{i,j} \cdot pL_j),$$

where pL_j is the size-specific capture probability estimate from equation (1) and $r_{i,j}$ and $M_{i,j}$ are the number of recaptures on pass 2 and marks applied on pass 1 in size-class j at site i, respectively. Note that this is equivalent to using the multinomial likelihood from Otis et al. (1978), but without estimation of N or consideration of the unmarked component of the population. We refer to the size-based capture probability model as L_3 (L indicates length, 3 the number of parameters that determine the capture probability for each size-class). This model collapses to a null model (L_1) in which capture probability is assumed to be constant across size-classes by removing the denominator in equation (1) and only estimating β.

We attempted to fit the size-based capture probability model (equation 1) to depletion data by aggregating catches across sites within 10-mm size-classes as for the mark–recapture data. However, parameter estimates for this model were very uncertain because, in the case of depletion data, it is necessary to jointly estimate the size of the aggregate population for each size-class as well as capture probability parameters. To avoid this problem yet still evaluate effects of size on capture probability, we first independently estimated capture probability and abundance for each size-class using the standard depletion model of Otis et al. (1978). We then fitted linear capture probability–fork length models to the estimates of capture probability and tested whether the slopes of these models were significantly different from zero. It was not necessary to transform capture probability estimates using logit or arcsine transformations prior to conducting regression analyses. Quantile–quantile plots showed that capture probability estimates were normally distributed, and only 5 of 108 estimates were less than 0.2 or greater than 0.8, for which the effects of transformation would be substantive (Gelman et al. 2004).

Evaluating effects of flow, habitat, and recovery period on capture probability.—We defined a series of candidate models that encompassed our hypotheses about the effects of sampling, habitat type, flow, and fish size on capture probability and then compared these models using an information-theoretic approach. We used the Akaike information criteria corrected for small sample size (AIC_c) for the comparisons. The AIC_c statistic is used to measure the amount of information lost among competing models by formally recognizing the tradeoff between bias and variance (Burnham and Anderson 2002). A more complex model with more parameters will almost always fit the data better than a simpler model with few parameters; however, the parameter estimates from the more complex model will be more uncertain. When comparing a range of candidate models, the model with the lowest AIC_c value is considered to have the best out-of-sample predictive power. Models with similar AIC_c values relative to the best model are considered to have strong support ($\Delta\text{AIC}_c = 0\text{–}2$), while those with larger AIC_c values are considered to have moderate ($\Delta\text{AIC}_c = 4\text{–}7$) or essentially no support ($\Delta\text{AIC}_c > 10$).

To evaluate the evidence for changes in capture probability across passes, we compared model D_1 with D_2 for depletion data and model MR_1 with MR_2 for mark–recapture data. As we compute the parameters for each experiment individually, we refer to these models as D_{1i}, D_{2i}, MR_{1i}, and MR_{2i}, respectively (the i subscript denotes individual estimates for each experiment). For each experiment, AIC_c was computed and compared across models, and the sum of experiment-specific AIC_c values was also compared. Note that AIC support criteria apply to all model comparisons, whether comparing two models for a single experiment or two models applied to a group of experiments. The AIC_c for the size-based capture probability model (L_3) was compared with the AIC_c from the model in which capture probability was assumed to be constant across size-classes (L_1). The effects of the combination of habitat and gear type on capture probability was evaluated by comparing models having common capture probabilities across all experiments and habitat types (D_{1c} or MR_{2c}, where c denotes a common habitat type) with more complex models that allowed capture probabilities to vary by habitat type (D_{1h} or MR_{2h}, where h denotes habitat-specific stratification). We refer to habitat-gear effects as habitat effects throughout the remainder of this paper and provide a rationale for this nomenclature in the discussion. Note that these models estimate common capture probabilities across groups of experiments, but experiment-specific population sizes. In the case of mark–recapture experiments, it was also possible to evaluate effects of habitat on size-dependent capture probability by comparing the sum of AIC_c values from habitat-specific relationships (model L_{3h}) with the AIC_c from a model that was common to both habitat types (model L_{3c}). As the asymptotic capture probability (β from equation 1) was similar across habitat types, we also compared L_{3c} and L_{ch} with a size-dependent model with habitat-specific means (μ) and SDs (σ) but a common asymptote (model $L_{2+,c}$).

The effect of flow on capture probability was evaluated by comparing models in which capture probability could vary across habitat types and across low- (September and November) and high-flow (June–August) months ($D_{1h(\text{mf})}$ or $\text{MR}_{2h(\text{mf})}$, where mf refers to stratification by monthly flow level) with simpler models in which capture probability could only vary by habitat type (D_{1h} or MR_{2h}). In the case of the depletion data, we were also able to compare models in which capture probability could vary across experiments conducted during the daily minimum and maximum discharges ($D_{1h(\text{df})}$, where df refers to stratification by the daily flow level) with models in which capture probability was constant across these strata (D_{1h}). Finally, for mark–recapture data, we evaluated the effect of the period between marking and recovery by comparing models in which capture probabilities could vary between 1- and 24-h experiments ($\text{MR}_{2h(\text{rp})}$, where rp refers to stratification by recovery period) with the simpler model in which capture probability was constant across these recovery periods (MR_{2h}).

Evaluating the effects of density on capture probability.—We examined the relationship between estimates of capture probability (p) and population density (N) to determine whether capture probability was density dependent. These parameter estimates can be negatively correlated owing to sampling error alone because larger estimates of N require smaller estimates of p (Schnute 1983). We therefore used a bootstrap procedure to test for density dependence in p following some of the methods of Speas et al. (2004). We simulated both three-pass depletion and two-pass mark–recapture data assuming binomial sampling error. The population sizes and capture probabilities used in the simulations were randomly selected from ranges that bounded the estimates from our data (simulated $p = 0.2\text{–}0.8$, $N = 10\text{–}200$ fish/100 m, site length = 50 m for depletion data from 2006; simulated $p = 0.05\text{–}0.8$, $N = 50\text{–}1{,}500$ fish/100 m, site length = 100 m for mark–recapture data from 2007). The most likely estimates of p and N for each set of simulated data were computed via a nonlinear iterative search procedure to minimize the log-multinomial likelihood as described above. The number of estimation failures was also determined. For depletion data, a failure was designated whenever the slope of the relationship between catch on each pass and the cumulative catch from previous passes was positive, or when the total catch across three passes was less than or equal to one. For mark–recapture simulations, a failure was designated whenever the number of fish caught on the first pass, or the number of marked fish recaptured on the second pass, was zero. The simulation–estimation procedure was repeated, and linear $p\text{–}\log_e(N)$ models ($p = a + b \cdot \log_e[N]$) were fit to the $p\text{–}N$ estimates for each level of simulated capture probability. Bias in capture probability estimates was computed by comparing the estimated values with the true simulated values (% bias = 100 × [estimated p − simulated p]/simulated p).

Comparisons of simulated and observed $p\text{–}\log_e(N)$ slopes were made via graphical and probabilistic approaches. For the graphical comparison, the observed $p\text{–}\log_e(N)$ slopes were compared with slopes based on simulated data, in which the latter slopes were computed from a fixed range of simulated capture probabilities (0.2, 0.4, 0.6, and 0.8) and random population densities within the ranges specified above. Two hundred and fifty trials were completed for each simulated capture probability. For the probabilistic comparison, cumulative frequency distributions (CFDs) of p–$\log_e(N)$ slopes were generated based on 100 trials of either 19 or 47 sets of simulated depletion data, and 7 or 35 sets of simulated mark–recapture data. These sample sizes reflect those available to estimate the p–$\log_e(N)$ slopes from our depletion or mark–recapture data in low- and high-angle habitats, respectively. Capture probability and density values used in the simulations were random draws from the ranges specified above. The value of the observed p–$\log_e(N)$ slope for each habitat type was then overlaid on the corresponding simulation-based CFD to determine the probability that the observed slope, or a steeper slope, could have arisen owing to chance alone. This probability is equivalent to a type I error rate (i.e., the probability of incorrectly rejecting the null hypothesis of no density dependence in capture probability).

Results

Population Closure and Capture Probability Estimates

There were very few captures of marked fish in 25-m shorelines bordering the downstream and upstream boundaries of mark–recapture sites. Capture of one or more marked fish in these areas occurred in two of seven experiments in low-angle habitat, and in 10 of 35 experiments in high-angle habitat. Incidences of marked fish being captured outside of the original sites were limited to the 24-h recovery experiments. Of 1,060 and 1,906 marked fish released in low- and high-angle habitats, respectively, only 0.47% ($n = 5$) and 0.68% ($n = 13$) were recaptured in adjacent areas. The total emigration rates in low- and high-angle habitats, estimated by expanding the number of marked fish captured in adjacent areas for each experiment by the estimated capture probabilities on the second pass (Figure 1), were 2.61% and 2.24%, respectively. Averaged across all mark–recapture experiments, there was an initial mortality due to electrofishing and capture of 8% (CV = 0.37) and 20% (CV = 0.57) in low- (backpack) and high-angle (boat electrofishing) habitats, respectively. Based on 24-h holding experiments, survival was 100% for all 194 fish captured by backpack electrofishing (96 stained fish and 98 clipped fish, fork lengths ranging from 30 to 74 mm), and for all 157 fish caught by boat electrofishing (85 stained fish and 72 clipped fish, fork lengths ranging from 40 to 110 mm).

There was essentially no support for the more complex depletion model that estimated different capture probabilities for the first and subsequent passes (D_2). Out of 66 experiments, there were only three cases in which the AIC_c from D_{2i} was lower than values from D_{1i} by more than two units. Summed across all experiments within habitat types, there was essentially no support for D_{2i} relative to D_{1i} in both low- and high-angle habitats (Table 4). In contrast, the AIC_c for MR_{2i} was lower than the AIC_c for MR_{1i} by more than two units in 21 out of 42 experiments, and there was strong support for MR_{2i} relative to MR_{1i} when the AIC_c values were summed across experiments (Table 5). The mean difference between capture probability estimates on the first pass and second passes across the 42 experiments was 0.03. This suggests that while there was strong evidence for variation in capture probabilities between the marking and recapture passes for individual experiments, there was no general tendency for either higher or lower capture probabilities on the second pass. Based on these results, we used models D_1 and MR_2 for subsequent analyses of depletion and mark–recapture data, respectively.

The average capture probability across 66 depletion experiments based on model D_{1i} was 0.54 with 80% of the estimates falling between 0.27 and 0.75 (Figure 1). The average capture probability on the first and second passes across 42 mark–recapture experiments based on model MR_{2i} was 0.31 and 0.28 with 80% of the estimates falling between 0.17 and 0.48 and between 0.16 and 0.43, respectively (Figure 1). The sampling error of the capture probability, indexed by the average of CVs from individual estimates, was 0.26 for both depletion and mark–recapture experiments.

Effects of Fish Size on Capture Probability

Size-dependent capture probability models based on mark–recapture data in low- and high-angle habitats (models L_{3h}) had strong support relative to models in which capture probability was assumed to be independent of size (models L_{1h}; Table 6). The logistic size-dependent capture probability models (equation 1) fit the length-stratified mark–recapture data well, explaining 90% of the variability in the MLEs of length-stratified recapture rates (Figure 2a). Fork length also explained 94% and 71% of the variation in capture probabilities from depletion experiments independently estimated for each size-class in low- and high-angle habitat, respectively (Figure 2b). The slopes of the relationships were significantly different than zero ($P = 0.006$ and 0.002, respectively).

Effects of Habitat on Capture Probability

The effect of habitat type on capture probability depended on data type and whether or not the effects of

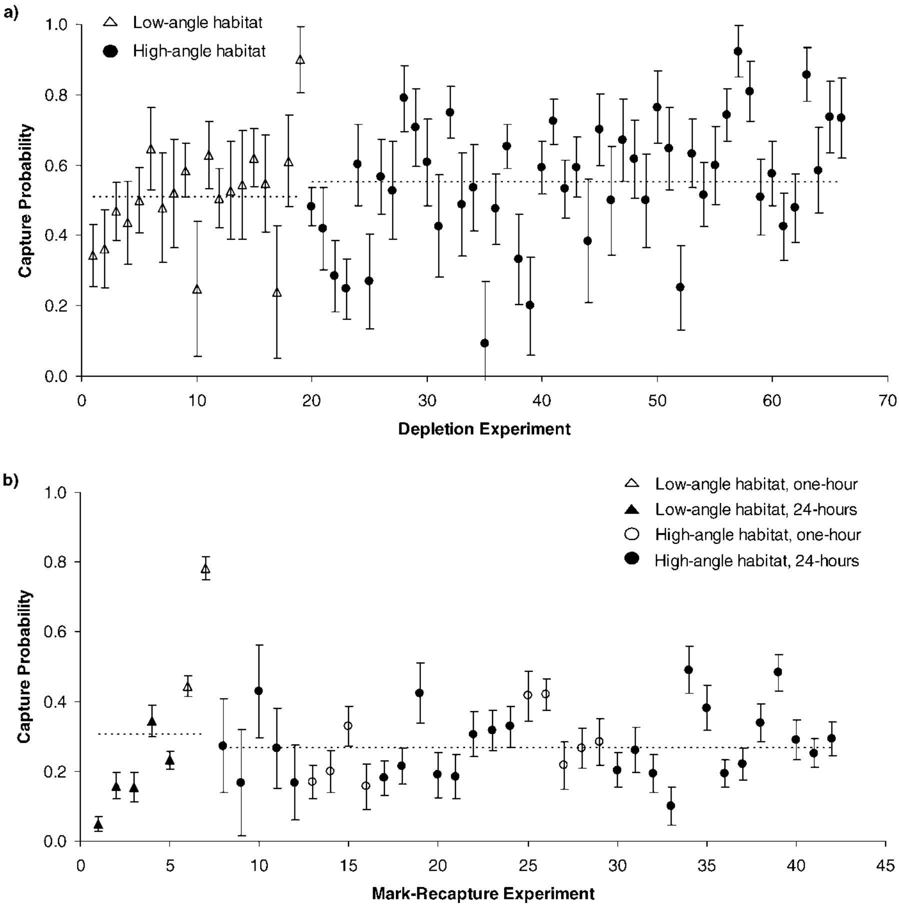

FIGURE 1.—Most likely estimates of capture probabilities from (**a**) depletion and (**b**) mark–recapture experiments (by experiment number) based on models D_{1i} and MR_{2i}, respectively (see text). Error bars denote the SEs of the estimates. The dashed lines represent the average capture probabilities in low- and high-angle habitats. Experiments are presented in chronological order within habitat types.

fish size were accounted for. Based on depletion data, there was strong support for both habitat-dependent (sum of AIC_c values for D_{1h} models across habitat types: $281.7 + 730.9 = 1{,}012.6$) and independent models ($D_{1c} = 1{,}010.5$), and the most likely estimates of the capture probabilities across habitat types were very similar (Table 4; Figure 3a). In contrast, there was strong support for habitat-specific capture probability models (MR_{2h}) relative to the habitat-aggregated model (MR_{2c}) based on mark–recapture data (Table 5). In this case, capture probability in low-angle habitat tended to be greater than that in high-angle habitat (Figure 3b), especially on the first pass (Table 5). A similar result was obtained from the size-stratified analysis (Table 6). There was strong support for the habitat-dependent models (L_{3h}) relative to the habitat-aggregated one (L_{3c}). The major difference between models in this case was the higher capture probability of small fish (lower μ) in the low-angle habitat type. Asymptotic capture probabilities (β) were similar among habitat types. As a result, the model which assumed that the β was constant across habitat types ($L_{2+,c}$) had slightly better predictive power than the model that allowed all three parameters to vary (Table 6).

Effects of Flow on Capture Probability

There was little evidence to suggest that flow influenced capture probability based on differences across flows within a day, but flow effects were somewhat confounded with the effects of fish size in the case of the across-month flow comparisons. The most likely estimates of capture probabilities based on depletion experiments at the daily minimum and maximum flows, and in high- and low-flow months

TABLE 4.—Summary of AIC results comparing alternate models applied to depletion data. The column headings p, k, LL, and AIC_c denote the most likely capture probability estimates, the number of parameters, the log likelihoods, and Akaike information criterion values adjusted for small sample size. Subscripts for model names denote the number of capture probabilities (1 = common across passes, 2 = different probabilities between the first and subsequent passes) and stratification (i = by experiment, h = by habitat type, df = by daily flow, mf = by monthly flow, and c = combined across habitat types). For brevity, the most-likely estimates for p for the experiment-stratified models are not shown, but the values for D_{1i} and MR_{2i} are shown in Figure 1; N denotes population size. See text for more details about the models.

Habitat	Model	Stratum	p	k	LL	AIC_c
		Model type (N and p estimated for each experiment)				
Low angle	D_{1i}			38	−106.4	294.3
	D_{2i}			57	−96.9	320.7
High angle	D_{1i}			94	−253.1	705.4
	D_{2i}			141	−234.4	776.8
		Flow and habitat effects (N estimated for each experiment but p common)				
Low angle	D_{1h}		0.50	20	−120.1	281.7
	$D_{1h(\mathrm{df})}$	Daily minimum	0.48	21	−119.6	282.8
		Daily maximum	0.54			
	$D_{1h(\mathrm{mf})}$	High flow	0.50	21	−119.9	283.4
		Low flow	0.55			
High angle	D_{1h}		0.51	48	−316.0	730.9
	$D_{1h(\mathrm{df})}$	Daily minimum	0.50	49	−314.1	729.1
		Daily maximum	0.57			
	$D_{1h(\mathrm{mf})}$	High flow	0.48	49	−311.5	724.0
		Low flow	0.57			
Combined	D_{1c}		0.51	67	−436.2	1,010.5

based on both depletion and mark–recapture data, differed by no more than 0.08 (Tables 4, 5; Figure 3a). Depletion models applied to data from low-angle habitat, which accounted for daily ($D_{1h(\mathrm{df})}$) or monthly ($D_{1h(\mathrm{mf})}$) effects of flow changes, had very similar AIC_c values to those from models that did not (D_{1h}; Table 4; Figure 3a). The addition of a flow effect resulted in a negligible improvement in fit as evidenced by almost equivalent log-likelihood values. In this case, the more complex flow-dependent models are not supported by the data even though the AIC_c values are close (see Burnham and Anderson 2002:131). Small differences in the magnitude of the flow effect reinforce this result (Figure 3a). A similar result was obtained for the daily flow change model in high-angle habitat ($D_{1h(\mathrm{df})}$). In contrast, there was moderate support for the monthly flow effect model in high-angle habitat ($D_{1h(\mathrm{mf})}$). However, in this case, fork length increased substantially between high- (July–August) and low- (September and November) flow months (Tables 2, 3), making it difficult to separate the effects of fork length and flow on capture probability. A similar result occurred for the monthly flow comparison in high-angle habitat from mark–recapture data (Table 5; $MR_{2h(\mathrm{mf})}$ versus

TABLE 5.—Summary of AIC results comparing alternative models applied to mark–recapture data. The abbreviation rp stands for recovery period; other abbreviations and subscripts are defined in Table 4.

Habitat	Model	Stratum	p_1	p_2	k	LL	AIC_c
		Model type (N and ps estimated for each experiment)					
Low angle	MR_{1i}				14	−129.3	286.8
	MR_{2i}				21	−93.3	229.1
High angle	MR_{1i}				70	−372.4	887.2
	MR_{2i}				105	−257.2	730.1
		Flow and habitat effects (N estimated for each experiment but ps common)					
Low angle	MR_{2h}		0.43	0.35	9	−195.5	409.1
High angle	MR_{2h}		0.29	0.29	37	−419.3	913.2
	$MR_{2h(\mathrm{mf})}$	High flow	0.26	0.29	39	−401.3	881.4
		Low flow	0.34	0.29			
Combined	MR_{2c}		0.34	0.31	44	−644.4	1,377.5
		Recovery period (N estimated for each experiment but ps common)					
Low angle	$MR_{2h(\mathrm{rp})}$	1 h	0.55	0.47	11	−131.7	285.6
		24 h	0.27	0.20			
High angle	$MR_{2h(\mathrm{rp})}$	1 h	0.28	0.30	39	−417.5	913.7
		24 h	0.30	0.29			

TABLE 6.—Summary of AIC results comparing alternate models applied to mark–recapture data stratified by 10-mm fork length-classes. Column headings β, μ, and σ denote the maximum, mean, and SD of the size–capture probability function (equation 1). See Tables 4–5 for additional details.

Habitat	Model	Stratum	β	μ	σ	k	LL	AIC$_c$
				Habitat and flow effects				
Low angle	L_{1h}		0.31			1	−139.9	281.9
	L_{3h}		0.34	26.61	2.60	3	−128.4	262.8
High angle	L_{1h}		0.29			1	−364.8	731.7
	L_{3h}		0.31	39.89	4.57	3	−348.5	703.0
Combined	L_{3c}		0.31	27.21	3.49	3	−492.5	990.9
	$L_{2+,c}$	Low angle	0.32	25.25	0.46	5	−477.4	964.8
		High angle	0.32	40.23	4.85			
High angle	$L_{3h(\mathrm{mf})}$	High flow	0.33	39.95	4.57	6	−345.5	703.0
		Low flow	0.30	45.00	0.00			
				Recovery period effect				
Low angle	$L_{3h(\mathrm{rp})}$	1 h	0.52	25.02	0.40	6	−82.4	176.9
		24 h	0.24	29.52	4.39			
High angle	$L_{3h(\mathrm{rp})}$	1 h	0.33	35.42	4.33	6	−341.5	695.0
		24 h	0.31	45.00	0.01			

MR_{2h}), mainly owing to higher capture probabilities during low-flow months on the first pass. The fish size–monthly flow effect confounding was also seen in the size-stratified analysis for high-angle habitat (Table 6), in which the increase in the number of parameters in the flow-stratified model ($L_{3h(\mathrm{mf})}$) relative to the model that did not account for flow (L_{3h}) was almost identical to the increase in the log likelihood across models. As a result, the AIC$_c$ values for both models were the same.

Effects of Recovery Period on Capture Probability

Capture probabilities based on 1-h recovery experiments tended to be higher than those from 24-h experiments, but the magnitude of differences depended on habitat type. The most likely estimate of capture probability on the second pass of mark–recapture experiments with a 1-h recovery period in low-angle habitat was over twice the value based on experiments with a 24-h recovery period (Table 5; Figure 3b). The model that accounted for recovery time was strongly supported relative to the model that did not. The capture probabilities for the 1- and 24-h recovery period experiments in high-angle habitat were very similar, and the difference in AIC$_c$ values between the models was negligible. However, in high-angle habitat, the distribution of 1-h recovery experiments was concentrated in early months when fish were smaller relative to the 24-h experiments (Table 3). Thus, the effect of recovery period was confounded with the effect of fish size. When the effect of size was accounted for by repeating the analysis using the size-dependent model, there was moderate support for the model that accounted for recovery period ($L_{3h(\mathrm{rp})}$) relative to the model that did not (L_{3h}; Table 6). There was strong support for the size-stratified recovery period model in low-angle habitat.

Density Dependence and Bias in Capture Probability

The effect of density on capture probability estimates depended on both habitat type and the method used to estimate capture probability. Based on depletion data, there was little evidence for density dependence in capture probability estimates in low-angle habitat, but strong evidence in high-angle habitat. Capture probability estimates were negatively correlated with estimates of $\log_e$ population density (Figure 4a, b; Table 7) and the slopes were significantly different than zero in both low- ($n = 19$; slope $= -0.136$; $P < 0.001$) and high-angle habitats ($n = 47$; slope $= -0.175$; $P < 0.001$). However, simulations revealed that the expected slope of the p–$\log_e(N)$ relationships due to sampling error increased as capture probability was reduced (Figure 4a, b [dashed lines]). Based on the bootstrap analysis of expected p–$\log_e(N)$ slopes, the probability that the observed slope of the p–$\log_e(N)$ relationship could be due to chance alone was 23% in low-angle habitat, but only 1% in high-angle habitats (Figure 5a). The difference in probabilities of density-dependent effects among habitat types was due both to the lower observed p–$\log_e(N)$ slope in low-angle habitat as well as the greater variance in the distribution of expected slopes because of smaller sample size.

For the mark–recapture experiments, there was strong evidence for density dependence in capture probability estimates in low-angle habitat but little evidence for this dynamic in high-angle habitat. The strength of the negative correlation between capture probability and $\log_e$ density varied by habitat type (Figure 4c, d; Table 7). In low-angle habitat, the slope

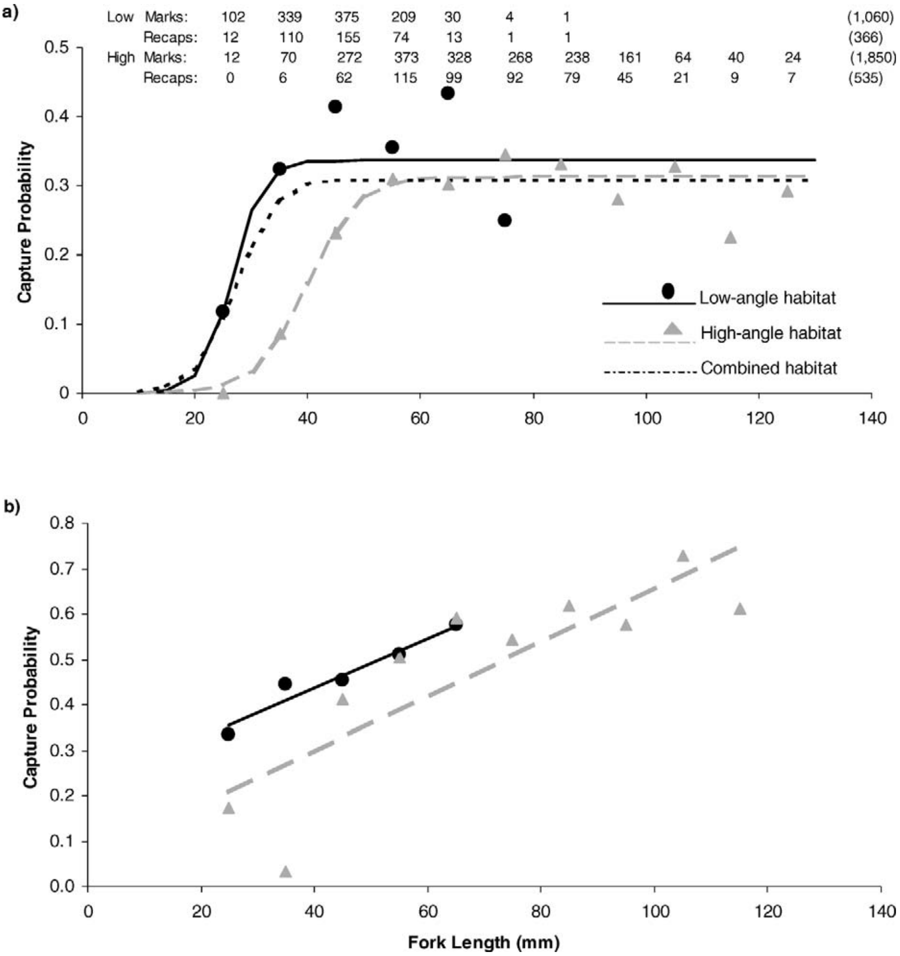

FIGURE 2.—Relationships between capture probability and fork length in low- (solid black lines) and high-angle (gray dashed lines) habitat types based on **(a)** mark–recapture and **(b)** depletion data. Panel (a) shows the best-fit logistic relationships (equation 1) with habitat-specific data as well as data combined across habitat types (black dashed line). The data points in represent the ratios of recaptured fish across experiments to the total number of marked fish, by 10-mm size-class and habitat type (i.e., independent Peterson estimates). The numbers at the top of panel **(a)** are the total marked fish and recaptures in each length class, along with the totals across length-classes (in parentheses). Note that the data point for the 85-mm length-class in low-angle habitat is not shown (capture probability = 1), as it exceeds the maximum value on the *y*-axis scale. In panel **(b)**, the data points are the best-fit capture probabilities independently estimated for each size-class; the lines show the best-fit linear relationships.

was steep and significant ($n = 7$; slope $= -0.249$; $P = 0.011$), while in high-angle habitat it was not ($n = 35$; slope $= -0.020$; $P = 0.42$). Simulations showed that when a large number of mark–recapture experiments are conducted ($n = 250$), there is little correlation between p and N (Figure 4c, d). This occurs because, unlike the case for depletion experiments, estimates of capture probability on the second pass are not dependent on population size because they are based on the recovery rate of a known number of marked fish. This difference also results in lower variance of the distributions of expected p–$\log_e(N)$ slopes based on mark–recapture relative to depletion experiments (Figure 5). The observed slope in low-angle habitat was relatively steep, and comparison with the CDF suggests there was a less than 1% probability that it could have arisen owing to chance alone. In contrast, the probability that the observed slope in high-angle habitat could be due to sampling error was 32%.

The correlation between density and fork length confounded the evaluation of the effects of density on capture probability. The $\log_e$ of density was signifi-

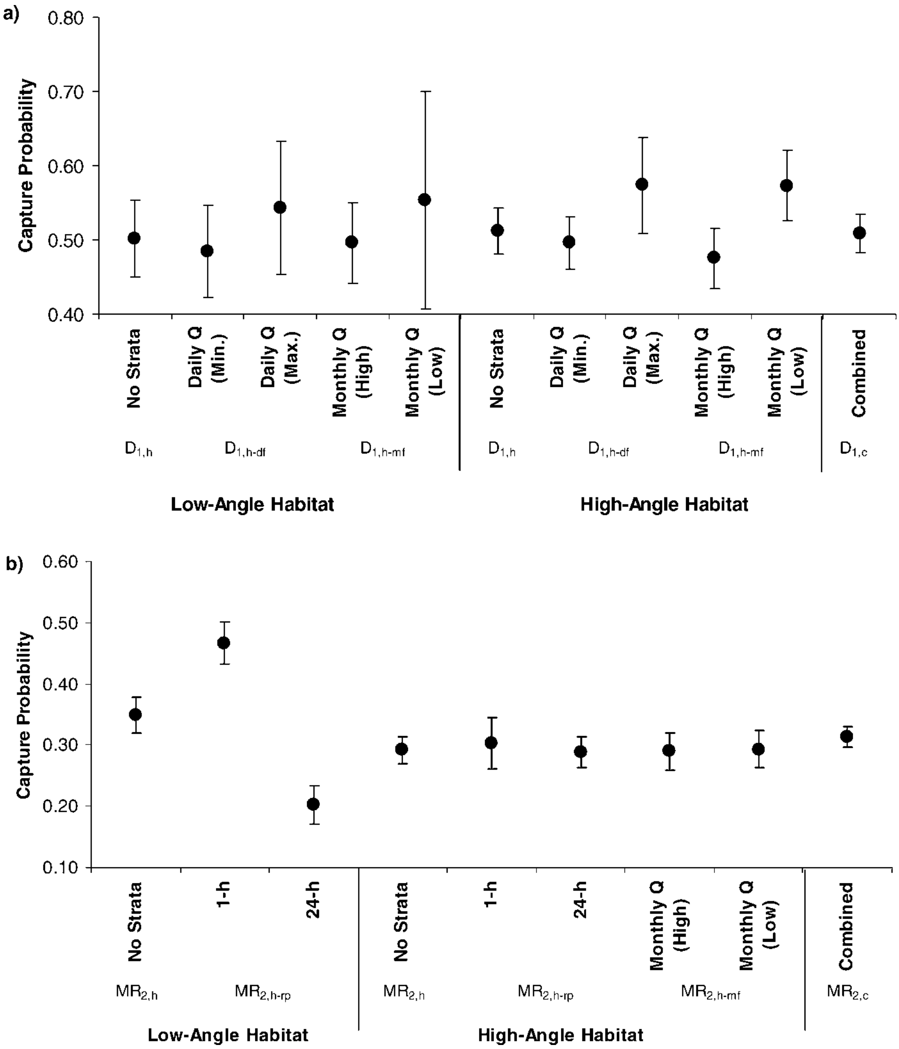

FIGURE 3.—Most likely estimates of capture probability from **(a)** depletion and **(b)** mark–recapture experiments in low- and high-angle habitat based on different models (see Tables 4–5). The error bars denote the 95% confidence intervals. The capture probabilities in panel (a) are based on the depletion model assuming the same capture probability across passes. The capture probabilities in panel (b) are based on the mark–recapture model assuming that capture probabilities differ across passes; values for the second pass are shown.

cantly negatively correlated with fork length based on data from both depletion and mark–recapture experiments in both habitat types (Table 7). This occurred because fish densities declined and fish grew over the sample period from early summer through late fall and because within sampling periods, populations at sites with higher fish densities tended to be comprised of smaller fish (Figure 4). The bootstrap analysis implied strong support for density dependence in capture probabilities based on depletion data in high-angle habitat and on mark–recapture data in low-angle habitat (Figures 4, 5). However, these were also the only cases in which the relationships between capture probability and fork length were both positive and significant (Table 7), and in which the confounding between size, density, and capture probability was apparent in the size-stratified capture probability–density relationships (Figure 4b, c).

Simulations demonstrated that capture probability is substantially overestimated from depletion data when the true capture probability is low and population size at discrete sites is small. Depletion estimation failure rates were 25%, and capture probability was overestimated by 54% at a simulated capture probability of

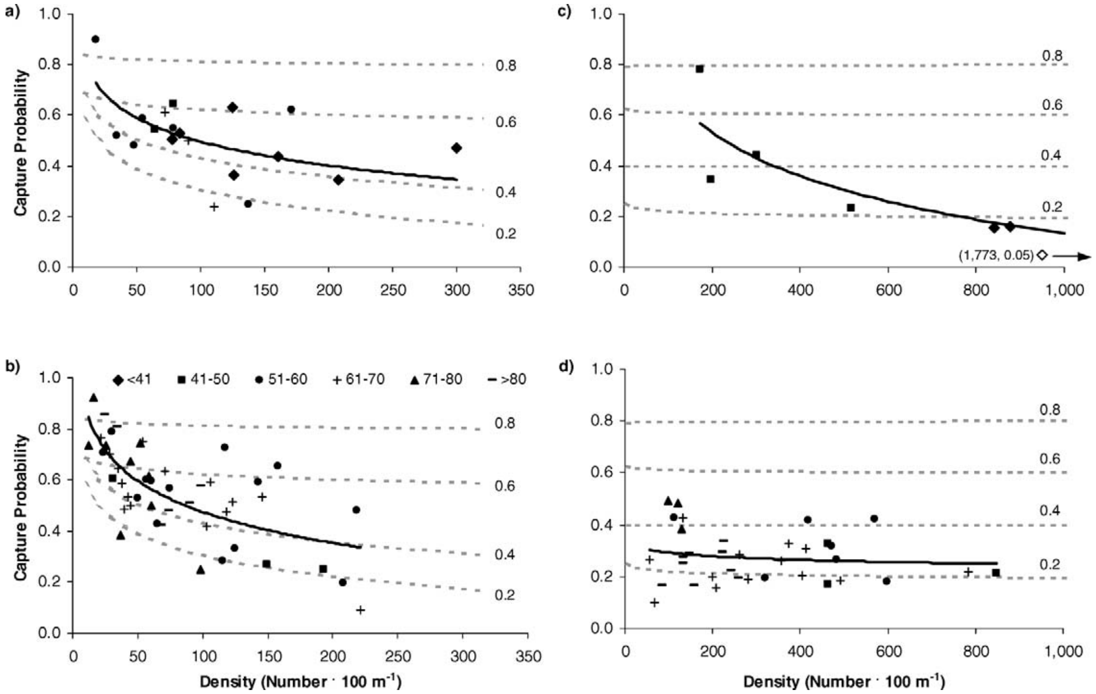

FIGURE 4.—Relationships between estimated capture probability and population density in **(a)** low- and **(b)** high-angle habitats from depletion experiments and **(c)** low- and **(d)** high-angle habitats from mark–recapture experiments. The symbols (see panel [b]) denote the average fork lengths on the first pass in 10-mm increments. The best-fit log-linear relationships to the estimates are shown as solid lines. The expected relationships due to sampling error under a range of simulated capture probabilities (0.2–0.8) and random densities are shown as the dashed lines. The open diamond in panel (c) denotes a point that is off the graph, the true coordinate being given in parentheses.

0.2 across the range of densities we simulated. The percent bias in capture probability (100 × [estimated value − simulated value]/simulated value) increased with decreasing population size when capture probability was 0.4 or less (Figure 4a, b [dashed lines]). At a simulated capture probability of 0.3 (which is close to the observed mean from mark–recapture experiments), capture probability was overestimated by 23%, and the estimation failure rate was 15% across the range of densities we simulated. Failure rate and bias in depletion estimates were minor or negligible at capture probabilities of 0.6 or more, regardless of density. In contrast, there was virtually no estimation failures or bias (<0.4%) at any of the simulated capture probabilities for mark–recapture experiments.

Discussion

This study has demonstrated that it is feasible to estimate capture probabilities for juvenile fish in a range of large river habitat types using a combination of backpack and boat electrofishing. Capture probabilities based on both depletion and mark–recapture experiments were reasonably precise (CV = 0.26). While the estimates from the depletion experiments

TABLE 7.—Pearson correlation coefficients for the relationships between $\log_e$ population density ($\log_e[N]$), capture probability (p), and fork length on the first pass (FL) based on depletion and mark–recapture data in low- and high-angle habitats; $0.01 < P \leq 0.05$*; $0.001 < P \leq 0.01$**; $P \leq 0.001$***.

Method	Habitat	Sample size	$\log_e(N)-p$	$\log_e(N)-$FL	$p-$FL
Depletion	Low angle	19	−0.59**	−0.48*	0.20
	High angle	47	−0.70***	−0.35*	0.29[a]
Mark–recapture	Low angle	7	−0.87*	−0.87*	0.77*
	High angle	35	−0.14	−0.48**	−0.10

[a] $P = 0.052$ for this correlation.

(mean $p = 0.54$) were higher than those from the mark–recapture experiments (mean $p = 0.31$ and 0.28 on the first and second passes, respectively), both were sufficiently large to allow reasonably precise estimation of population sizes at discrete sites. Capture probability increased with fish size in both mark–recapture and depletion experiments, and field data supported the assumption that populations within discrete sites can be treated as effectively closed.

Given that capture probability has been shown to decline with increasing stream size (Peterson et al. 2004; Rosenberger and Dunham 2005), one might expect capture probability to be low in larger river systems like the Colorado River. Our data suggest that this is not the case, as capture probability estimates were within ranges reported for smaller streams. Eighty percent of depletion-based estimates were between 0.28 and 0.75, similar to ranges reported for juvenile brown trout (0.4–0.6; Wyatt 2002), bull trout *Salvelinus confluentus* and cutthroat trout *O. clarkii* (0.2–0.6; Peterson et al. 2004), and rainbow trout (0.5–0.65; Rosenberger and Dunham 2005). Eighty percent of mark–recapture-based estimates of capture probability fell between 0.17 and 0.45, a range similar to those reported for bull trout and cutthroat trout (0.1–0.3; Peterson et al. 2004) and rainbow trout (0.3–0.5; Rosenberger and Dunham 2005). The range in our capture probability estimates was larger than the ranges reported in other studies, perhaps because we sampled age-0 trout over the growing season, in which fish size, and therefore vulnerability to capture, changed substantially.

Data from holding and mark–recapture experiments supported the fundamental assumption that populations at discrete sites are effectively closed. Holding experiments showed that there is very likely negligible mortality of marked fish after release for at least 24 h. In large rivers, it is not logistically feasible to enclose mark–recapture or depletion sites with stop nets as is commonly done in small streams. However, capture of marked fish in 25-m sections adjacent to mark–recapture sites was extremely rare, indicating that populations within sites can be treated as effectively closed for the 24-h period between release and recapture. This conclusion is supported by studies that show limited effects of electrofishing (Dunham et al. 2002) and electrofishing-based capture and marking (Mitro and Zale 2002; Young and Schmetterling 2004) on salmonid movement, as well as those showing that salmonids tend to have very restricted movements over short and sometimes extended time periods (e.g., Edmundson et al. 1968; Roni and Fayram 2000; Rodriquez 2002). It is certainly possible that some marked fish moved beyond the 25-m lengths of shoreline that was sampled upstream and downstream of mark–recapture sites, and that we therefore underestimated the extent of emigration and capture probability. However, the proportion of a population that is displaced over increasing large distances is well described by a steep negative slope (see the meta-analysis of Rodriquez 2002). Considering that there were few individuals found within the 25-m shoreline areas bordering the mark–recapture sites, the number of fish that migrated further than this distance must be very small and would therefore have a minor effect on capture probability estimates. In addition, had emigration out of depletion and mark–recapture sites been a significant problem in our study, capture probability estimates should have been lower than those reported for smaller streams in which sites were enclosed with stop nets, which was not the case.

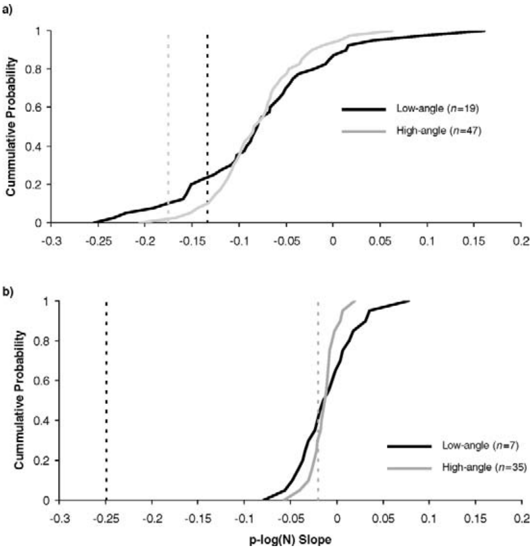

FIGURE 5.—Cumulative frequency distributions of the expected slopes of the capture probability–log population density relationship ($p = a + b \cdot \log_e[N]$) generated from simulated data (solid lines) compared with those of the slopes fit to the data (vertical dashed lines [slopes of the solid lines in Figure 4]) based on **(a)** depletion and **(b)** mark–recapture data. The distributions were computed by estimating slopes from 100 sets of simulated data based on the actual sample sizes of 19 (low angle; black lines) and 47 (high angle; gray lines) to represent depletion experiments and seven (low angle) and 35 (high angle) to represent mark–recapture experiments.

There was strong evidence from mark–recapture and depletion experiments that capture probability increased with fish size. A positive relationship between fish length and electrofishing capture probability, such as the ones estimated in this study from mark–recapture data, is consistent with many other investigations (Borgstrom and Skaala 1993; Anderson 1995; Bayley and Austen 2002; Peterson et al. 2004) and is not surprising considering larger fish have a greater head-to-tail voltage potential in an electric field, are easier to see and net, and make less use of interstitial spaces relative to smaller fish and are therefore easier to capture. However, the relationship between size and capture probability should be estimated for each specific study, as the functional form can be variable, ranging from linear (e.g., Borgstrom and Skaala 1993), to logistic (Peterson et al. 2004; this study), to dome shaped (Bayley and Austen 2002). The form and parameters will probably depend on the range of fish sizes available for capture, gear type, habitat, environmental variables, and fish behavior.

We found significant differences in capture probability across habitat types from mark–recapture experiments. Capture probability tended to be higher in low-angle habitat sampled by backpack electrofishing. The mean of the size–capture probability function in high-angle habitat sampled by boat electrofishing ($\mu = 39.9$ mm) was greater than in low-angle ($\mu = 26.6$ mm) habitat sampled by backpack electrofishing, which implies lower vulnerability of smaller fish in high-angle habitat, a result consistent with depletion data. This was probably caused by the larger interstitial spaces between talus blocks in high-angle shorelines, making it more difficult to see and retrieve very small fish that were stunned, and because the very immediate shoreline areas utilized by smaller fish could be more effectively sampled with a backpack electrofisher than a boat electrofisher. Our evaluation of "habitat" effects on capture probability could perhaps be more accurately described as a comparison of "habitat and gear type" effects. We argue that such a distinction is irrelevant; what matters is that capture probability be quantified by habitat type, regardless of whether different gears, or ways of using the same gear, are employed. Or stated more broadly, it is not necessary to use the same gear to quantify relative habitat use as long as the differences in capture probability between specific combinations of habitat and gear are accounted for.

We found that flow did not affect electrofishing capture probability. Physical conditions within immediate nearshore habitats in the Lee's Ferry reach are not very sensitive to flow, at least over the range experienced in this study. Measurements of nearshore (1.5 m from shore) average water column velocities across 24 sites in 2004, taken at discharges of 260 (daily minimum flow) and 500 (daily maximum flow) m^3/s (very close to the range in this study; Table 1), differed by no more than 3–6 cm/s (see Table 1 from Korman and Campana 2009). In large rivers, the velocities in the immediate nearshore environment that can be sampled by electrofishing are less influenced by discharge than those in smaller rivers because the ratio of nearshore sample width to the total wetted width is much lower. We suspect this is why our capture probability estimates were relatively insensitive to the effects of flow, and perhaps why capture probability has been shown to be sensitive to indices of flow (such as cross-sectional area) in smaller systems (e.g., Rosenberger and Dunham 2005).

The effects of fish density on capture probability were challenging to discern, variable among habitat types and estimation methodologies, and confounded with the effect of fish size. Using bootstrap simulation, we concluded there was a significant relationship in high-angle habitat based on depletion data, and in low-angle habitat based on mark–recapture data. However, these were also the cases in which a negative correlation between fish size and density was most apparent. Density-dependent growth in stream-dwelling populations of age-0 salmon and trout has been well documented (e.g., Armstrong 1997; Jenkins et al. 1999; Imre et al. 2005), and will result in a negative correlation between density and fish size among sites sampled within a short time interval, and among sites sampled through time. Cumulative growth and mortality over the growing season will also result in a negative correlation between density and fish size based on samples collected through time, even in the absence of density-dependent growth (e.g., Elliott 1994). Effects of density and fish size on capture probability are separable by manipulations of size and density in artificial ponds or streams (e.g., Bayley and Austen 2002). In field studies of juvenile fish such as the one presented here, it will probably be very difficult to empirically separate the effects of fish density and size on capture probability. However, this difficulty is not necessarily a problem in assessments of juvenile abundance if the size–density relationship is stationary, and the relationship between size and capture probability is accounted for in the estimation of capture probabilities.

The capture probabilities determined from depletion experiments were on average 80% higher than those based on mark–recapture. Results from the simulation study and previous investigations strongly suggest that the latter estimates are more realistic. Positive bias in capture probabilities estimated from the depletion method occurs because of both model misspecification and the nature of the likelihood function. There was not enough information in the depletion data to select a removal model that allowed capture probability to decline with successive passes, or even between the first pass and later ones. However, it is well recognized that the power of such tests is generally very low (Otis et al. 1978; Rosenberger and Dunham 2005). Failure to account for declining capture probability across successive passes of electrofishing has been shown to result in overestimates in capture probability of 39% for bull trout and cutthroat trout (Peterson et al. 2004), and 30–50% for rainbow trout (Rosenberger and Dunham 2005), with the extent of bias being greater for smaller fish that generally have lower capture probability. Our simulations showed that even if capture probability is constant over passes, it can still be substantially overestimated if population size and capture probability are low. For example, at a true capture probability of 0.3, capture probability will be overestimated by 25% at densities of 100 fish/100 m (or 50 fish in a typical 50-m site). This bias occurs because the multinomial likelihood function used in Otis et al. (1978) is derived from probabilities associated with finite samples, and these probabilities depend on sample size (Schnute 1983). For example, the probability of obtaining five heads of a perfectly balanced coin flipped 10 times will be higher than the probability of obtaining 50 heads if it is flipped 100 times. Thus, when jointly estimating capture probability and population size in the depletion method by maximizing the likelihood function, slightly higher probabilities occur at lower population sizes, resulting in the tendency to overestimate capture probability. The combined bias associated with model misspecification reported from previous studies, and from the likelihood function estimated in this study, implies our depletion-based estimates of capture probability are approximately 50–75% too high. The 80th percentile range of capture probability estimates from depletion experiments (0.28–0.75), adjusted for biases of 50% and 75%, were 0.19–0.50 and 0.16–0.43, respectively. These ranges are much closer to the range from our mark–recapture experiments of 0.18–0.37.

We recommend that mark–recapture experiments, rather than depletion experiments, be used to estimate capture probabilities for juvenile fish in large rivers. Our recommendation is similar to those from recent studies conducted in smaller systems (Peterson et al. 2004; Rosenberger and Dunham 2005; Sweka et al. 2006). Over the range of capture probabilities and population densities experienced in this study, simulation results showed that values determined from depletion experiments were probably substantially overestimated owing to the likelihood function. Differences between mark–recapture and depletion estimates suggest there was additional bias due to changing capture probability over passes, a dynamic that could not be detected from the depletion data alone. Direct estimation of size-dependent capture probabilities should be a fundamental component in the evaluation of juvenile populations if fish size has the potential to vary substantially over the study period or among study sites. Mark–recapture experiments have a distinct advantage over depletion methods in this respect because they do not require the estimation of abundance by size-class, reducing the number of parameters that need to be estimated. Finally, mark–recapture experiments allow for field-based validation of key closure assumptions. These assumptions must be evaluated when electrofishing at discrete sites owing to the potential for latent mortality and emigration after release. In this study, we did not test whether marked fish had the same capture probability as unmarked fish. We are currently evaluating this assumption by using different gear types for capture (dipnetting via snorkeling) and recapture (e.g., electrofishing) passes, an approach that cannot be used in depletion studies unless capture probability is allowed to vary among passes. Although our study was based only on juvenile rainbow trout, it is likely that the general approach and recommendations are applicable to a wide range of fish species.

The dynamics of capture probability for juvenile fish are complex because they depend in large part on patterns of behavior and habitat use that occur over a wide range of temporal and spatial scales. For example, in this study we showed that daily changes in flow do not influence capture probability within immediate nearshore zones that were sampled. However, in a companion paper (Korman and Campana 2009) we show that most age-0 trout in the Lee's Ferry reach do not migrate with the waters edge as it rises and falls over a 24-h period with changing discharge. At the daily maximum flow, most fish remain further offshore closer to or within the portion of the channel that is continuously wetted over 24 h. As a result, fish densities within the immediate nearshore zones that are sampled at the daily maximum flow were 50–80% lower than when sampled at the daily minimum. Thus, if we define capture probability as the proportion of fish that are caught over a cross section of the river or on a reachwide basis, rather than within the immediate shoreline zone of sampling areas (as in this study), flow can have an effect on capture probability because of its influence on fine-scale patterns of habitat use. In a long-term study of recruitment dynamics in the Lee's Ferry reach (Korman 2009), we have controlled for this effect by sampling only at the daily minimum flow, which is why most of the depletion and mark–recapture experiments in this study were conducted at the minimum flow. The long-term study has also clearly documented an ontogenetic habitat shift from low- to high-angle shorelines that occurs over a period of a few months. Had we only used backpack electrofishing to sample age-0 trout, a tactic common to many juvenile fish assessments in rivers, our sampling universe would have been restricted to low-angle shorelines. Estimates of capture probability in this habitat type over the growing season, which would increase with fish size, would not detect the reachwide decline in capture probability that results from an increasing proportion of the population moving to habitats outside of the sampling universe. Thus, to make valid reach- or systemwide assessments of juvenile fish populations, it is not sufficient to simply estimate capture probability at discrete sites that are logistically or financially efficient to sample. Rather, sampling and capture probability estimation should be conducted over the full range of habitats that are used over the period of interest, which, in many cases, will probably require use of more than one gear type and considerably more effort than is commonly applied.

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