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[Article]

Evaluation of Removal Sampling for Basinwide Assessment of Atlantic Salmon

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Abstract.—Removal estimators for stream fish abundance are widely used but can result in biased population estimates at the site level. We conducted computer simulations to examine how the Carle and Strub (1978) estimator, coupled with variation in catchability, influences the accuracy of population estimates at the site level. Site-level population estimates were then used to examine what effect potential bias in the population estimate at a site had on basinwide abundance estimates. Historic electrofishing data collected from Atlantic salmon *Salmo salar* in the Narraguagus River, Maine, were used as the baseline for construction of these simulations. At the site level, mean percent bias of population estimates was −23% when catchability was low (0.30–0.40) and when the true population was low (1–20 fish). Bias was reduced as the true population size increased and catchability increased. The negative bias at the site level affected total population estimates for the entire river basin. Under current sampling methodology in the Narraguagus River, basinwide population estimates are probably 11–17% lower than the true population. Confidence intervals (95%) would be expected to cover the true population between 65% and 79% of the time. Increasing the amount of sampling had little effect on the negative bias of basinwide population estimates but did reduce the error around the estimate, as expected. These results should serve as a reference point for gauging the effectiveness of current sampling efforts in providing reliable estimates of Atlantic salmon parr in the Narraguagus River. The methodology employed by this simulation study can also be applied to other Atlantic salmon rivers to evaluate current sampling programs.

Maximum-likelihood multiple-pass electrofishing estimates (Carle and Strub 1978) are used for population assessments of parr of Atlantic salmon *Salmo salar* in Maine rivers and in the Connecticut and Merrimack River basins. Abundance estimates at the site level are then extrapolated to the basin level to estimate watershed-wide fish production. The accuracy of removal estimators depends on the catchability during each electrofishing pass. Catchability is a function of the experience and equipment of the electrofishing crew, changes in fish behavior between electrofishing passes (Mahon 1980; Schnute 1983; Peterson and Cederholm 1984; Peterson et al. 2004), size of the fish (Reynolds 1989; Anderson 1995), and habitat complexity and stream flow (Rodgers et al. 1992; Thompson and Rahel 1996). Removal estimators (e.g., Zippin 1956, 1958; Carle and Strub 1978; White et al. 1982) are negatively biased and this bias is most significant if there is a large decline in capture efficiency between electrofishing runs. The body of literature on bias in depletion estimators is growing, and some are cautioning against use of multiple-pass depletion estimates in favor of other unbiased approaches to population estimation (e.g., Peterson et al. 2004). Previous work has focused on evaluating bias in individual site estimates of fish abundance. However, the effects of this bias on composite population estimates extrapolated to an entire stream or basinwide level has not received much attention.

To evaluate current sampling methodology and

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TABLE 1.—Stratification scheme for basinwide Atlantic salmon parr abundance estimation in the Narraguagus River, Maine (J. Kocik, NMFS, personal communication).

Stratum	Region	Habitat	Number of potential sites	Average site size (m^2 [SD])	Mean number of sites sampled per year (range)
110	Upriver forested	Run	77	719 (391)	5 (4–6)
120	Upervier forested	Riffle	16	1,103 (345)	2 (1–2)
210	Forested barrens	Run	83	449 (114)	4 (2–4)
220	Forested barrens	Riffle	81	683 (221)	2 (2–3)
310	Transitional barrens	Run	133	671 (308)	5 (5–5)
320	Transitional barrens	Riffle	148	626 (482)	2 (1–3)
410	Coastal	Run	153	584 (180)	7 (5–7)
420	Coastal	Riffle	119	759 (293)	6 (5–7)
500	West Branch	Combination	60	1,042 (464)	1 (1–2)
600	Primary use tributaries	Combination	36	403 (123)	5 (4–6)
700	Intermittent tributaries	Combination	107	404 (133)	1 (1–1)

make sampling recommendations, we sought a better understanding of the estimator at the basin level. The objective of this study was to use computer simulations to evaluate current sampling methodology on the Narraguagus River aimed at estimating basinwide Atlantic salmon parr abundance. We were specifically interested in how potential bias of the removal estimator influenced site-level population estimates and the effect this would have on population estimates of Atlantic salmon for the river basin as a whole.

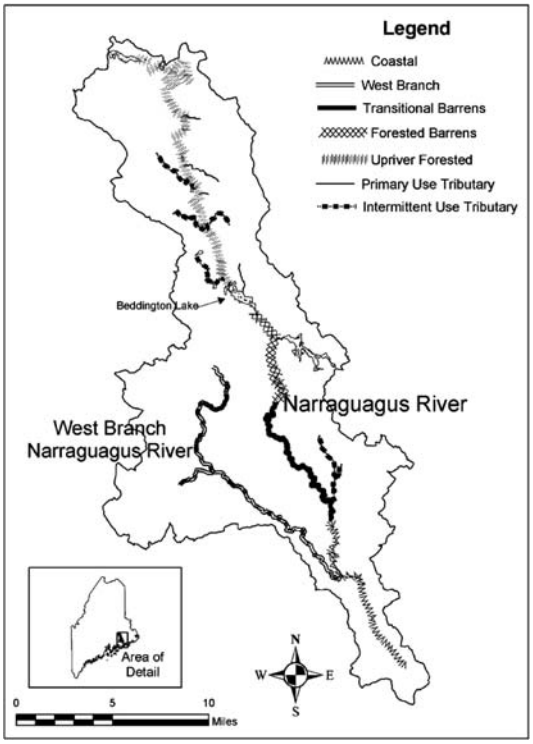

FIGURE 1.—Map of the Narraguagus River watershed, Maine, showing stratification for basinwide Atlantic salmon parr abundance estimation (courtesy of J. Kocik, National Marine Fisheries Service).

Methods

Historic Narraguagus River sampling.—The Narraguagus River is one of the most extensively sampled rivers in Maine for assessment of Atlantic salmon age-1 parr abundance. In recent years (mid-1990s to present), the river has been stratified according to geographical location and habitat type (Table 1; Figure 1) to facilitate more precise estimates of total parr abundance in the basin (J. Kocik, National Marine Fisheries Service, personal communication). There are 11 strata, and the average number of sites sampled per stratum has ranged from one to seven per year. Sites have ranged from 200 m^2 to greater than 2,000 m^2 in size, depending on stratum and stream width. Each site is typically sampled using multiple-pass depletion with two to five electrofishing passes, and block nets are placed at the upstream and downstream ends. Sampling is conducted during August and September, when stream flows are at base flow conditions. Historic population estimates using the Carle and Strub (1978) estimator have ranged from 0 to more than 180 parr. Parr abundance estimates and associated variance are calculated for each stratum according to the methods of Hankin (1984). Total abundance and variance in the river basin as a whole are then calculated as the sum of strata estimates.

Simulations of Narraguagus River sampling.—The Narraguagus River basin was modeled from historical Atlantic salmon parr electrofishing data. The number of potential sites (N) within a stratum was estimated by dividing the total available habitat area of a particular stratum by the average size of a site within that stratum (Table 1). For these simulations, the known population at a site was simulated by fitting historic population estimates to a negative binomial distribution for each stratum. The negative binomial distribution was chosen

so that the population at a site would be bounded by 0, and this distribution generally provided the best fit to historical abundance estimates over all strata. The known population of age-1 parr at each site within each stratum was then chosen randomly from each stratum's respective negative binomial distribution (Table 1). The total simulated population for the entire Narraguagus River was 17,545 age-1 parr.

Once the sampling universe was established, 10,000 simulations of six scenarios were conducted. These scenarios consisted of combinations of three levels of sampling effort and two levels of changes in catchability. First, the number of sites chosen within each stratum (n) equaled the mean number historically sampled in each stratum (Table 1). Sites were chosen randomly by simple random sampling without replacement. The other two levels of sampling effort increased the sample size within strata by a factor of two ($2 \times n$) and five ($5 \times n$).

For each of the sample size scenarios, two scenarios of catchability (p) were simulated. In the first scenario, p was allowed to vary randomly between 0.30 and 0.75 for each site according to a uniform distribution and this randomly chosen level was held constant between successive electrofishing passes. Historic estimates of p using the Carle and Strub (1978) estimator have been as high as 0.96 for multiple-pass depletions (Maine Atlantic Salmon Commission, unpublished data), but these may be overestimates as removal estimators tend to overestimate true catchability (Peterson et al. 2004). A few historic mark–recapture population estimates have been made in the Narraguagus River, and the probability of recapturing marked individuals ranged from 0.30 to 0.73. Thus, the range of 0.30–0.75 seems reasonable for the range of true p in these simulations. Variability in the number of fish captured on each electrofishing pass was incorporated by assigning a random number from a uniform distribution (0, 1) to each fish at a site during each of three simulated electrofishing passes. If the random number of a fish on a particular pass was less than the randomly chosen p for the site, the fish was assumed captured on that pass. If a fish was captured on one pass, it was not available for potential capture in subsequent passes. This method allowed the total number of fish actually captured for a given level of p to vary. For example, if a site had a population of 50 individuals and a p of 0.50, between 38 and 48 fish would be captured by the end of the third pass 90% of the time. For the second scenario of catchability, p was again randomly chosen from the above range, but it was decreased at an assumed rate of 10% between electrofishing passes to simulate declining capture efficiency with successive capture events. For example, if p equaled 0.30 on the first pass, p equaled 0.27 on the second pass.

The Carle and Strub (1978) estimator was used to calculate the population estimate at a site:

$$Z = \frac{\hat{Y}+1}{\hat{Y}-T+1} \prod_{i=1}^{k} \left[\frac{K\hat{Y}-X-T+\beta+(K-i)}{K\hat{Y}-X+\alpha+\beta+(K-i)} \right], \tag{1}$$

where Z = an intermediate statistic in the Carle and Strub (1978) estimator, $\hat{Y}$ = estimated population size, K = number of capture events, T = total number of animals in event i, $X = \sum_{i=1}^{k}(K-i)C_i$, C_i = number of animals captured in event i, and α and β = parameters of the prior beta distribution, both set to 1.0 for a uniform prior. The population size was found by searching for the lowest $\hat{Y}$ that produced a Z-value of 1.0 or less. The total number of animals captured, T, was used as a lower bound for $\hat{Y}$ in the search.

The variance of the population estimate was estimated by Zippin (1956):

$$\hat{\sigma}^2 = \frac{\hat{Y}(1-\hat{p})^K[1-(1-\hat{p})^K]}{[1-(1-\hat{p})^K]^2 - K^2\hat{p}^2(1-\hat{p})^{K-1}}, \tag{2}$$

where $\hat{p} = \frac{T}{K\hat{Y}-X}$.

Population estimates from each of the above simulations were then used to estimate the total population of each stratum and associated variance assuming sites were of equal size and chosen by simple random sampling (Hankin 1984):

$$\hat{Y}_s = \frac{N}{n}\sum^{n}\hat{Y}_i; \tag{3}$$

$$\hat{V}(\hat{Y}_s) = \frac{N_s(N_s-n_s)\sum^{n}(\hat{Y}_i-\hat{\bar{Y}}_s)^2}{n_s(n_s-1)} + \frac{N_s\sum^{n}\hat{\sigma}_i^2}{n_s}, \tag{4}$$

where $\hat{Y}_s$ = total population in stratum s, $\hat{Y}_i$ = population estimate at site i, N_s = the number of potential sites in stratum s, n_s = the number of sites sampled in stratum s, $\hat{V}(\hat{Y}_s)$ = variance of the stratum s total population estimate, $\hat{\bar{Y}}_s = \sum\hat{Y}_i/n_s$ = mean population estimate in stratum s, and $\hat{\sigma}_i^2$ = the variance of the Carle and Strub (1978) population estimate at site i.

Even though electrofishing sites actually vary in size in the Narraguagus River, we chose not to use a ratio estimator (Hankin 1984), which accounts for site size in the population estimate. Historic electrofishing data did not meet the assumption of a strong positive correlation between site size and abundance estimates required by the ratio estimator. Also, with the relatively

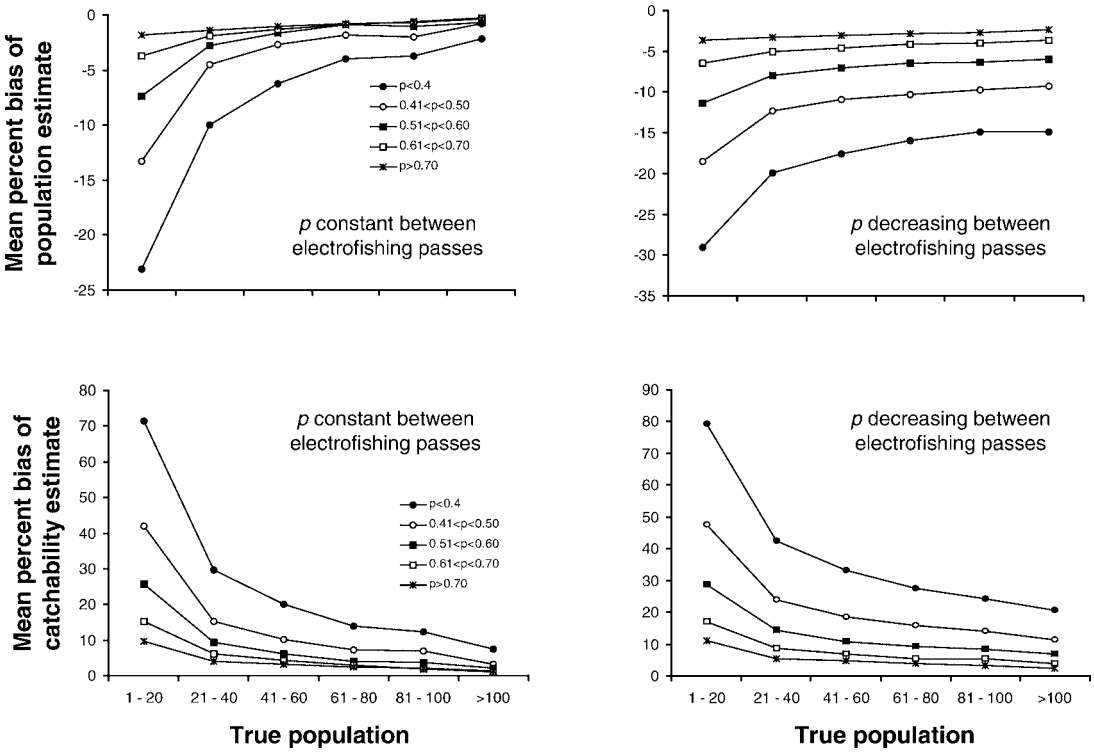

FIGURE 2.—Site-level bias of Atlantic salmon parr population estimates and catchability estimates for various ranges of true catchability (p) and true population size. Overall mean bias (±SD) of site-level population estimates was −8.03 ± 19.22% for constant catchability and −12.97 ± 19.96% for decreasing catchability.

small numbers of sites sampled per stratum, estimates of the variance can have serious negative bias (Cochran 1977). Our simulations thus assumed that all sites were equal in size.

The total population estimate and associated variance for the basin was the sum of the strata estimates and strata variances:

$$\hat{Y}_B = \hat{Y}_1 + \hat{Y}_2 + \ldots + \hat{Y}_s; \quad (5)$$

$$\hat{V}(\hat{Y}_B) = \hat{V}(\hat{Y}_1) + \hat{V}(\hat{Y}_2) + \ldots + \hat{V}(\hat{Y}_s). \quad (6)$$

Assessment of abundance estimates.—Bias of the simulated population estimates was assessed at both the site and basinwide levels. Bias at the site level was indexed by the difference between the Carle and Strub (1978) population estimate for a site and the true population at that site. For the simulations of "historic n, constant p" and "historic n, decreasing p," data were grouped into arbitrary bins of increasing true population size (increments of 20 fish) and p (increments of 0.10). Mean percent bias was calculated for simulated population estimates in each of these bins. Mean percent bias was also calculated for estimates of p in the same manner. Bias at the basinwide level was indexed by the difference between the basinwide population estimate and the true population for the basin. Confidence intervals (95%) were approximated for basinwide abundance estimates as $t_{0.025,d} \cdot \sqrt{\hat{V}(\hat{Y}_B)}$ using a Satterthwaite approximation of the appropriate degrees of freedom (Thompson 1992). The percentage of the time the 95% confidence limits fell above, covered, or fell below the true basinwide population was calculated for each set of simulations

Results

Site-Level Abundance Estimates.

The Carle and Strub (1978) estimator gave negatively biased abundance estimates at the site level. Overall, mean percent bias for site-level population estimates was −8.03 ± 19.22% when catchability was held constant and −12.97 ± 19.96% when catchability decreased between electrofishing passes. Mean percent bias was greatest in situations of low true population size (1–20 parr) and low catchability ($0.30 < p < 0.40$) (Figure 2). As the population size, catchability, or both increased, bias was reduced. Negative bias was less

TABLE 2.—Mean bias (SD) and mean relative standard error of simulated basinwide population estimates in the Narraguagus River, Maine. Coverage refers to the percentage of the simulations in which the 95% confidence interval (CI) on the basinwide estimate fell above, covered, or fell below the true basin population.

Capture efficiency	Sample size	Mean basinwide bias (SD)	Mean relative standard error (SD)	Coverage of true population by 95% CI		
				Above	Cover	Below
Constant	Historic n	−11.47 (13.04)	0.28 (0.05)	0.26	78.74	21.00
	2 × historic n	−10.07 (9.52)	0.23 (0.06)	0.04	80.17	19.79
	5 × historic n	−8.64 (5.27)	0.13 (0.01)	0.00	68.77	31.23
Decreasing	Historic n	−17.04 (12.07)	0.28 (0.05)	0.05	64.57	35.38
	2 × historic n	−15.45 (8.84)	0.23 (0.06)	0.00	61.99	38.01
	5 × historic n	−14.28 (4.82)	0.12 (0.01)	0.00	25.42	74.58

than 5% when either the population exceeded 60 fish or catchability exceeded 0.60 when catchability remained constant among electrofishing passes at a site. In the simulations where catchability decreased at a rate of 10% between successive electrofishing passes, bias was greater than in the simulations where catchability was held constant between electrofishing passes. Negative bias was less than 5% only when the initial catchability on the first electrofishing pass exceeded 0.60 and the true population exceeded 40 fish. These results indicate that potential decreases in catchability due to behavioral changes of the fish can increase the inherent negative bias of removal estimators.

Estimates of catchability were overestimated using the Carle and Strub (1978) method (Figure 2). Mean percent bias of $\hat{p}$ was 71% in situations of low catchability ($0.30 < p < 0.40$) and small population size (1–20 parr). As Atlantic salmon parr abundance and true catchability increased, estimates of $\hat{p}$ were less biased. In the simulations where true catchability decreased at a rate of 10% between electrofishing passes, the mean percent bias of $\hat{p}$ increased over that seen in the simulations where true catchability was held constant between electrofishing passes. Note that the plots in Figure 2 do not show smooth curves as seen in similar plots in Carle and Strub (1978). This is due to unequal sample sizes when combinations of population size and p were binned, resulting in some bins having small sample sizes and hence not estimating bias and precision very well.

Basinwide Abundance Estimation.

The negative bias found at the site level was also seen when site-level population estimates were extrapolated to basinwide total population estimates. Mean percent bias was −11.47% from the simulations using the historic mean sample size per stratum and constant catchability between electrofishing passes (Table 2). This bias increased to −17.04% when catchability decreased between electrofishing passes. Increasing the number of sites sampled per stratum had minimal effect on mean percent bias in both scenarios of constant catchability and decreasing catchability. If catchability actually remains constant between electrofishing passes on the Narraguagus River and the current sample size is increased by a factor of five, the true population may still be underestimated by an average of −8.64% (Table 2).

Coverage of the true basinwide population by 95% confidence limits varied among the different simulations (Table 2). Increasing the sample size from the historic n to $2n$ had little effect on coverage of the true basinwide population by 95% confidence limits. However, increasing the sample size to $5n$ decreased coverage and increased the percentage of time that 95% confidence limits fell below the true basinwide population. This effect was more pronounced under the decreasing catchability scenario (Table 2). Under current sampling efforts on the Narraguagus River, managers can expect that confidence limits of basinwide Atlantic salmon parr estimates cover the true population 65–79% of the time depending on whether catchability changes between electrofishing passes. In all cases, when 95% confidence limits did encompass the true population, this coverage tended to be by the upper confidence interval, as indicated by the negative mean percent bias of the point estimate.

The precision of basinwide Atlantic salmon parr abundance estimates increased when the sample size in each stratum doubled (Table 2). Mean relative standard error decreased from approximately 0.28 using the historic sampling effort in each stratum to approximately 0.13 when sampling effort was increased by a factor of five. This result was expected under sampling theory; that is, increased sample size decreases variance. Constant versus decreasing catchability between electrofishing passes had virtually no influence on the precision of basinwide parr estimates.

Discussion

Our results at the site level mirror those of other studies that have shown removal estimators are

negatively biased, especially when catchability does not remain constant (White et al. 1982; Riley and Fausch 1992; Peterson et al. 2004). Also, catchability could be overestimated even when the true catchability was held constant in the simulations here. Catchability for the Carle and Strub (1978) estimator is determined after the population estimate is obtained by the equation $\left(\hat{p} = \frac{T}{K\hat{Y}-X}\right)$. When the true population is underestimated by $\hat{Y}$, then the denominator of this equation decreases, thus overestimating the true catchability.

Another way to introduce bias into the site-level estimate is to round the Z-value in equation (1). The Z-value was not rounded by Carle and Strub (1978) but has been rounded to one decimal place by others (Lockwood and Schneider 2000). Rounding this value always results in a population estimate less than or equal to the estimate when the Z-value is not rounded. Simulation of rounding versus not rounding demonstrated a clear bias due to rounding (C.M.L., unpublished data). All results presented here did not round the Z-value.

The negative bias observed at the site level was also apparent as site-level population estimates were extrapolated to a stratum, and stratum estimates were summed for basinwide population estimates. Overall mean bias (±SD) at the site level (−8.03 ± 19.22% for constant catchability; −12.97 ± 19.96% for decreasing catchability) was similar to mean bias when site-level population estimates were extrapolated to the basinwide level for the historic amount of sampling effort (−11.47 ± 13.04% for constant catchability; −17.04 ± 12.07% for decreasing catchability). Although the Carle and Strub (1978) estimator generally underestimates the true population size, there are occasions when the population size is overestimated. We initially thought the occasional overestimates at some sites would dampen the effect of underestimates at most sites when both are combined to estimate the population at a larger scale. This was not the case, however, and relative bias at the site level resulted in similarly biased basinwide estimates. Also, increasing sampling effort had minimal effect on the relative bias of basinwide estimates.

Management Implications

Atlantic salmon managers in New England should be aware that population estimates obtained via removal sampling are negatively biased at both the site level and basinwide level. Basinwide population estimates of Atlantic salmon parr are desirable so that estimates of overwinter survival to the smolt stage can be made (NMFS and USFWS 2005). In estimating survival to the smolt stage, dividing a smolt population estimate obtained by stratified mark–recapture sampling (e.g., Darroch 1961; Dempson and Stansbury 1991) by an underestimate of parr abundance will result in an overestimate of survival from parr to smolt stages. A population viability analysis for Maine Atlantic salmon by Legault (2005) demonstrated that survival at all life stages is important for long-term sustainability. If parr-to-smolt survival is overestimated, managers may make wrong assumptions as to the relative importance of various life-stage-specific survival rates in the conservation of this species.

If basinwide population estimation of Atlantic salmon parr is to continue as a population assessment tool, then managers should modify sampling protocols to decrease negative bias. Three options to reduce negative bias include (1) increasing the number of electrofishing passes and use of a removal estimator that allows catchability to vary (e.g., the generalized removal estimator described by Otis et al. 1978); (2) development of capture efficiency models for various habitats and flow conditions (e.g., Peterson et al. 2004); and (3) use of mark–recapture estimators (e.g., Peterson and Cederholm 1984). All of these methods require additional sampling effort and for basinwide population estimates of parr, the gain in reducing bias may be compromised by the reduction in the number of sites that can be sampled for a fixed level of effort. One way to evaluate the appropriateness of various population estimation techniques is to compare the mean square error (MSE) of the estimate, which combines variance and bias $(MSE(\hat{Y}) = V(\hat{Y}) + bias(\hat{Y})^2)$. If a Petersen mark–recapture estimator were used, sampling crews would need to return to the same site on two consecutive days, thereby reducing total effort within the watershed by approximately half. Decreasing sampling effort by half increases the extrapolation portion of the strata variance estimate in equation (4), $\left(\frac{N_s(N_s-n_s)}{n_s}\right)$, by approximately a factor of two if the fraction of total sites sampled is small (<20%). Peterson and Cederholm (1984) found Petersen mark–recapture estimates were 8% less biased than removal estimators for juvenile coho salmon *Oncorhynchus kisutch*. However, this decrease in bias is not enough to decrease mean square error of the estimate due to increased variance from greater extrapolation.

Basinwide Atlantic salmon parr abundance estimates should be best viewed as an index of abundance rather than an estimate of absolute abundance. Our simulation results suggest that confidence intervals on basinwide age-1 parr population estimates under historic sampling levels in the Narraguagus River include the true population 79% of the time at best (if catchability actually remains constant between electrofishing passes). The mean relative standard error for this simulation

is ±28%. This level of error may be too large to detect yearly differences in parr abundance or to evaluate changes in management activities for the basin as a whole. The ability to track changes in parr abundance may be better served by not trying to estimate absolute abundance, but rather by developing sampling strategies that minimize the error on an index of relative abundance. An example of such a sampling strategy could be stratified estimates of mean catch per unit effort (Crozier and Kennedy 1994) with strata incorporating various levels of stream morphology and habitat complexity. The assumption of using such an index is that catchability is constant through time. Although it would be difficult to test this assumption in the field throughout an entire river basin, sampling under low flow conditions during late summer and early fall, combined with stratification of sampling according to habitat complexity, makes this a reasonable assumption.

The results of these simulations not only agree with what others (White et al. 1982; Riley and Fausch 1992; Peterson et al. 2004) have found concerning negative bias of removal estimators and overestimation of catchability by removal sampling but also evaluated the effects of potential negative bias on total population estimates when site-level population estimates are extrapolated to a large spatial scale. This type of simulation modeling is a useful tool to explicitly examine bias in population estimation techniques of ongoing sampling schemes. It is also useful for cost–benefit analysis at different levels of sampling effort. Managers can then use this information to evaluate the quality of their population estimates and the value of such data in making and evaluating management actions.

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