

Hankin and Reeves' Approach to Estimating Fish Abundance in Small Streams: Limitations and Alternatives

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Abstract.—Hankin and Reeves' (1988) approach to estimating fish abundance in small streams has been applied in stream fish studies across North America. However, their population estimator relies on two key assumptions: (1) removal estimates are equal to the true numbers of fish, and (2) removal estimates are highly correlated with snorkel counts within a subset of sampled stream units. Violations of these assumptions may produce suspect results. To determine possible sources of the assumption violations, I used data on the abundance of steelhead *Oncorhynchus mykiss* from Hankin and Reeves' (1988) in a simulation composed of 50,000 repeated, stratified systematic random samples from a spatially clustered distribution. The simulation was used to investigate effects of a range of removal estimates, from 75% to 100% of true fish abundance, on overall stream fish population estimates. The effects of various categories of removal-estimates-to-snorkel-count correlation levels ($r = 0.75$ – 1.0) on fish population estimates were also explored. Simulation results indicated that Hankin and Reeves' approach may produce poor results unless removal estimates exceed at least 85% of the true number of fish within sampled units and unless correlations between removal estimates and snorkel counts are at least 0.90. A potential modification to Hankin and Reeves' approach is the inclusion of environmental covariates that affect detection rates of fish into the removal model or other mark–recapture model. A potential alternative approach is to use snorkeling combined with line transect sampling to estimate fish densities within stream units. As with any method of population estimation, a pilot study should be conducted to evaluate its usefulness, which requires a known (or nearly so) population of fish to serve as a benchmark for evaluating bias and precision of estimators.

Fish populations are typically monitored with abundance estimates. The traditional approach to estimating stream fish abundance involves the selection of sites (i.e., sampling units) within a stream and the subsequent counting of fish within those sites. Sampling units can, for example, be defined as pools, riffles, and glides. Surveyed sites are either selected randomly or are chosen based on how well they represent the population of interest. Two of the more widely used methods to obtain within-unit estimates of stream fish abundance are snorkeling (Dolloff et al. 1996) and electrofishing (Reynolds 1996).

Building on earlier work by Hankin (1984), Hankin and Reeves (1988) developed a double sampling approach that employed both snorkeling and electrofishing for estimating fish abundance in small streams. In this approach, a stream is first stratified by habitat type (e.g., riffles, pools, and glides) and reach location (e.g., lower, middle, and

upper), and then a systematic sample with a single random start is selected within each stratum. Visual estimates of fish numbers are obtained concurrently by two divers snorkeling within each selected unit. Multiple-pass electrofishing removals within a systematic subsample of the randomly-selected units provide a "true" fish count based on Zippin's (1958) estimator. The removal estimates are then used in a ratio estimator (Cochran 1977) to adjust for incomplete detection of fish by snorkel counts in the non-electrofished units.

Hankin and Reeves' (1988) approach has been applied in stream fish work across North America, including studies monitoring threatened and endangered species. A recent search of the Science Citation Index (Institute of Scientific Information, Philadelphia) identified 45 articles that have cited the Hankin and Reeves paper, although the number of papers describing research that employed their approach is probably lower. As with any method of population estimation, however, key assumptions underlying Hankin and Reeves' approach must be met for the abundance estimator to be minimally biased and reasonably precise. Here, I outline these assumptions, describe various factors that may lead to violation of the assumptions, and use a simulation modeling approach to evaluate

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the degree to which the assumptions can be violated and still produce minimally biased and reasonably precise results. In addition, I offer a both a potential modification and an alternative to Hankin and Reeves' approach, which represent possible avenues of future research and development. I concentrate on Hankin and Reeves' method of abundance estimation, because their method of mapping sampling units performed reasonably well in field tests by Roper and Scarnecchia (1995).

Key Assumptions and Potential Violations

Key assumptions of the Hankin and Reeves' (1988) approach involve the ratio estimator used to correct snorkel counts for incomplete detection of fish within snorkeled units. The assumptions include: (1) fish within electrofished units are counted completely, and (2) the relation between removal estimates and average diver snorkel counts within surveyed units is strongly linear.

Removal Estimates as Complete Counts

Hankin and Reeves (1988) equated Zippin's (1958) removal estimator with a complete count of fish within sampled units. Important assumptions underlying this estimator include: (1) constant electrofishing effort during each sampling occasion, (2) no births (or immigration) or deaths (or emigration) during the sampling period (closure assumption), and (3) identical capture probabilities of fish within and among sampling occasions (Otis et al. 1978; White et al. 1982). Previous studies based on known numbers of fish indicated that Zippin's removal estimates underestimated true abundances by 13–52.5% (Bohlin and Sundstrom 1977; Peterson and Cederholm 1984; Rodgers et al. 1992; Riley et al. 1993).

Use of standardized protocols for applying equal effort within sampling units may satisfy the constant effort assumption, at least approximately. Riley and Fausch (1992) suggested that constant effort could be attained by thoroughly sampling all habitats within each pass, which would be especially important within sampling units with high habitat complexity.

Block nets can help ensure population closure by providing physical barriers during electrofishing passes, to minimize or eliminate fish movements to areas beyond the unit boundaries. Fish in small streams can exhibit a flight response to electrofishing current, causing them to move outside the sampled area (e.g., brown trout *Salmo trutta*; Nordwall 1999). For instance, 52% of 52

marked, 100–299-mm trout *Salvelinus* spp. moved 50–100 m (fish could not move beyond the physical barriers at 100 m) in response to electrofishing conducted in a second-order stream in Washington (N. P. Banish, J. T. Peterson, and R. F. Thurow, U.S. Forest Service, Boise, Idaho, unpublished preliminary report). Closure assumption violations of this type will lead to a negatively biased removal estimator (White et al. 1982; Kendall 1999). The magnitude of the bias will depend on the relative numbers of fish moving out of the sampling unit. Hankin and Reeves (1988) made no mention of block nets in their field study; if block nets were not used, Hankin and Reeves' removal estimates may have been much lower than actual abundances. In fact, block nets also would be required for snorkeled units, because flight responses of fish to divers could lead to spurious results if enough fish moved outside the unit boundaries.

Identical fish capture probabilities within and among sampling occasions will never be exactly met under field situations. Capture rates of fish sampled via electrofishing will vary with factors such as fish density, fish behavior and size, habitat structure, environmental conditions (e.g., stream temperature, turbidity, etc.), sampling gear, and sampling unit size (e.g., Northcote and Wilkie 1963; Mesa and Schreck 1989; Rodgers et al. 1992; Bayley and Dowling 1993). These factors can vary both spatially and temporally. Although identical capture probabilities are unattainable in typical field conditions, removal methods may nevertheless produce useful results in situations of high capture probabilities and large population sizes (e.g., two-pass removal estimates greater than 0.6 for over 200 fish and greater than 0.8 for over 100 fish; Bohlin 1982).

Linear Relation between Removal Estimates and Snorkel Counts

An unbiased ratio estimator requires a straight-line relation between removal estimates (assumed true counts) and snorkel counts that passes through the origin, as well as a proportional relation between variability in removal estimates and snorkel counts (Cochran 1977). Confidence intervals based on the normal distribution apply for large samples. In practice, at least 30 samples for both the removal estimates and the snorkel counts are required for the confidence intervals to reach nominal level. Otherwise, variances and confidence interval widths will be underestimated (Cochran 1977).

A more or less proportional relation between the

TABLE 1.—Estimated correlation coefficients (r) between snorkel counts and multiple-pass removal estimates of smaller size-classes (70–100 mm) of brook trout, bull trout, cutthroat trout, and rainbow trout in 35 small streams sampled in north-central Idaho and southwestern Montana (R. Thurow, U. S. Forest Service, unpublished data).

Species	Number of streams	Number of stream sections	r
Brook trout	8	14	0.38
Bull trout	25	65	0.20
Cutthroat trout	16	25	0.20
Rainbow trout	17	50	0.44

variances of removal estimates and snorkel counts seems at least approximately attainable. An increased variance is expected in counts with increased numbers of fish. Conversely, correlations between snorkel counts and removal estimates will be affected by factors influencing sightability or catchability of fish within and among surveyed units (e.g., habitat structure, fish density, etc.). Therefore, consistently high correlations between snorkel counts and removal estimates are not a certainty, despite the extremely high correlation coefficients (r) reported by Hankin and Reeves (1988) for juvenile coho salmon *Oncorhynchus kisutch* ($r = 0.95$ for pools and 0.99 for riffles) and juvenile steelhead *O. mykiss* ($r = 0.61$ for pools and 0.98 for riffles). For instance, correlations between snorkel counts and multiple-pass removal estimates were low ($r = 0.20$ – 0.44) for smaller size-classes (70–100 mm) of brook trout *S. fontinalis*, bull trout *S. confluentus*, cutthroat trout *O. clarki*, and rainbow trout *O. mykiss* sampled in 35 streams in north-central Idaho and southwestern Montana (Table 1). The lower the correlation coefficient, the more biased the ratio estimator.

Simulations

I used computer simulations to investigate effects of different levels of violations of the two key assumptions underlying Hankin and Reeves' (1988) approach. I evaluated their ratio estimator based on 95% confidence interval coverage (percentage of intervals that contained the true abundance), which potentially addressed problems with bias and precision, and a coefficient of variation ($CV = 100 \times SD/mean$) averaged across all simulation runs. White et al. (1982) considered a CV less than 20% to be reasonably precise. The Statistical Analysis System (SAS Institute 2000) was used to perform all simulations.

Details

I generated a spatial distribution of counts within a sampling frame configured from Hankin and Reeves' (1988) example application, except I used only five strata ($N = 62$ – 67 sampling units) because no fish were observed in the sixth stratum (upper riffles) in their example. The spatial distribution corresponded to a standardized Morisita index (Morisita 1962; Smith-Gill 1975) of 0.51, to incorporate population clustering at the 95% confidence level (Krebs 1999). This approach was used to mimic spatial clustering of fish populations due to such factors as heterogeneity in stream habitats and behavior of fish. Total steelhead abundance within each stratum matched those estimated by Hankin and Reeves (1988).

Each simulation run produced a stratified systematic sample of units of known fish abundance. Within each unit, some proportion of fish was detected by two divers. Fish detection rates for diver counts were randomly chosen from the range of 0.2 to 0.6, which was approximately that reported by Rodgers et al. (1992). I used Hankin and Reeves' (1988) example results to specify the general range and relation (diver differences) of these counts. I assumed diver counts within units were independent, as in Hankin and Reeves' example. Further, removal estimates were assigned to equal some proportion of the true counts within sampled units; these categories included 75–80%, 80–85%, 85–90%, 90–95%, 95–99%, and 100% removal. I also incorporated increased variances in removal estimates with larger diver counts. Correlation coefficients were computed for removal estimates and average diver counts for each simulation run and were placed in the following five categories: 0.75–0.80, 0.80–0.85, 0.85–0.90, 0.90–0.95, and 0.95–1.0.

I conducted enough simulation runs to generate 2,000 population estimates, confidence intervals, and coefficients of variation for each combination of removal and correlation categories. This often required very large numbers of runs (e.g., >750,000) for lower-valued categories because of low abundances within strata and correspondingly low counts within many units of those strata. Due to the paucity of count data, statistics could not be produced for all strata when removal estimates were less than complete counts. In these cases, overall population estimates and related statistics were calculated from fewer than five strata.

Results

When removal estimates equaled true numbers of fish within sampled units, 95% confidence in-

terval coverage averaged about 90% (range 89–91%) with an average coefficient of variation equal to 17.3–17.6% for correlation categories 0.9–0.95 and 0.95–1.0. Conversely, coverage was lower (range 82–87%) for correlation categories between 0.75 and 0.90. By extrapolation, correlation coefficients less than 0.75 would have exhibited even poorer confidence interval coverage. In general, confidence intervals did not reach the nominal rate of coverage (>94%), mainly because there was a less-than-perfect linear relation between removal estimates and diver counts, sample sizes were less than 30, and spatial clustering led to an underestimation of the single systematic sample variance based on random sampling (i.e., the sampling method assumed a random spatial distribution of individuals; Scheaffer et al. 1990).

Simulation results were mixed when removal estimates were lower than true abundances. When removal estimates represented at least 85% of true abundances within sampled units, confidence interval coverage was close to nominal or above (>94%) for all correlation categories, but precision was relatively low (coefficient of variation = 26.8–29.4%), which would widen confidence intervals and hence increase coverage. In addition, low stratum abundances precluded use of all but one stratum (lower pools) for generating estimates. Conversely, confidence interval coverage was much poorer for categories in which removal estimates represented lower proportions of unit abundances. Coverage ranged from 78% to 86% for categories of removal estimates that were 75–85% of true unit abundances across all correlation categories, with the coefficient of variation equal to 18.9–21.0% and based on three to four strata.

Potential Improvements to Hankin and Reeves' Approach

Within the data context of Hankin and Reeves' example application, simulation results indicated that Hankin and Reeves' (1988) approach may produce poor results unless removal estimates exceed at least 85% of the true number of fish within sampled units and unless correlations exceed 0.90. Therefore, in this section, I discuss a potential modification and alternative to their approach when these conditions cannot be met in the field, which probably occurs often. I emphasize that these suggestions are not offered as definitive remedies, but rather as possible avenues for further research and development. Any untested methods of abundance estimation should be subjected to

field trials and validated with a known population prior to full implementation.

Mark-Recapture Models and Individual Covariates

A possible modification to Hankin and Reeves' approach is to replace Zippin's removal model, which is a mark-recapture model incorporating a trap response (i.e., model M_b ; Otis et al. 1978; White et al. 1982), with another type of mark-recapture model. Within the mark-recapture framework, a number of available models relax various assumptions related to capture probabilities of individuals, including a generalized removal model (model M_{bh}) that accounts for heterogeneity in capture probabilities. Further, individual covariates that represent the most important factors affecting fish capture probabilities should be included in the mark-recapture model. The covariates must be measured at each surveyed unit. Analogous applications have been suggested both for aquatic systems (Bayley 1993) and for terrestrial environments (Pollock et al. 1984; Samuel et al. 1987; Steinhorn and Samuel 1989; Manly et al. 1996). Huggins (1989, 1991) developed mark-recapture models that allow for individual covariates; these models have been incorporated into the software program MARK (White and Burnham 1999).

Variance estimates produced by mark-recapture models typically are not corrected for overdispersion, resulting in underestimation of the true variance by as much as two to three times (Bayley 1993). Quasi-likelihood (Wedderburn 1974) theory often is used as a basis for correction of overdispersed data (Cox and Snell 1989; McCullagh and Nelder 1989). At present, MARK does not provide a variance inflation factor (Cox and Snell 1989) that corrects for overdispersion in this class of models, but it does allow users to specify different values of the variance inflation factor (G. White, Colorado State University, personal communication).

Line Transect Sampling

Line transect sampling has been broadly applied to both terrestrial and marine species, but rarely to freshwater aquatic organisms. Ensign et al. (1995) applied line transect methods via snorkeling to estimate abundance of benthic stream fishes, but the authors did not compare their results to a known population; hence, the usefulness of this technique within streams remains in question. Here, I briefly review the three key assumptions

underlying the line transect sampling method and offer potential remedies for problems associated with snorkel counts of fish in small streams. Buckland et al. (2001) provided a detailed overview of distance sampling in theory and in practice. The software program DISTANCE (Laake et al. 1993; Thomas 1999) is available for analysis of line transect and other distance sampling data.

The critical assumptions for line transect sampling are: (1) every individual present on the transect is detected, (2) distances are measured to each detected individual's original location (or distance category), and (3) distances (or distance categories) are measured without error. In practice, detecting every fish on a line may be problematic, depending on the size-classes sampled. Smaller fish may be hidden in the substrate and hence undetectable to the snorkeler. Such a problem may be minimized if a species' presence in the water column is strongly correlated with time of day. For instance, bull trout may be more visible to snorkelers at night than during the day (Peterson 2000). Methods exist that correct for incomplete detections on the line, but these typically require independent observers operating simultaneously (see Buckland et al. [2001] for a review of different methods). Note that Hankin and Reeves' (1988) approach also requires independence of diver counts.

Responsive movements of fish to a snorkeler may be minimized by implementation of proper snorkeling protocol. For instance, when moving slowly and carefully, snorkelers can approach close enough to identify individual rainbow and cutthroat trout during the daytime without causing a flight response (J. Guzevich, U.S. Forest Service, personal communication). In addition, bias related to fish movements will be minimized if the movements remain within a given distance category (see below).

Distance measurements to mobile individuals are more likely to be accurate if distances are recorded in categories. Snorkelers can use a calibrated mask-bar (Swenson et al. 1988) or similar device to estimate distance categories to detected fish, as long as they can either maintain a constant height above the streambed or record this height with every distance measurement. A somewhat analogous approach was used in aerial line transect surveys by Johnson et al. (1991), in which marks on the airplane struts corresponded to a given distance from the line to a sighted object on the ground, when measured from known heights.

Proper survey design also is important in line

transect sampling (Buckland et al. 2001). For the density estimator to remain unbiased for the entire area of interest, lines must be randomly placed within a stream or stream-habitat unit. Moreover, lines should be placed parallel to the perceived density gradient of fish. That is, if fish abundance increases much more from shore to shore than in an upstream or downstream direction, then transects should be oriented across the stream rather than along the stream. However, such an arrangement may be inefficient for small streams. Therefore, a zigzag or sawtooth design (Buckland et al. 2001) from shore to shore may be chosen instead, to increase transect lengths and spatial coverage while still capturing the gradient change.

Discussion

Within the simulation framework used in this paper, Hankin and Reeves' (1988) approach provided poor confidence interval coverage for population estimates when removal estimates were less than 85% of true abundances in subunits used to correct for units with snorkel counts alone. Previous studies have indicated that removal estimates can underestimate true abundance by more than 50% (e.g., Riley et al. 1993). Although Hankin and Reeves recognized the shortcomings of using removal estimates in place of complete counts, they still believed their approach was a practical alternative for estimating fish abundance in small streams. Nonetheless, the assumption that electrofishing produces complete counts should be evaluated before the Hankin and Reeves approach is fully implemented. In addition, researchers should evaluate the correlation between removal estimates and snorkel counts to ensure that a strong linear relation is present.

When evaluating the usefulness of removal estimates, researchers should remember not to confuse high precision with low bias. Low capture probabilities and population sizes (or violation of model assumptions) may yield highly precise abundance estimates that are far from the true population value. This results in what Anderson et al. (1998) described as "highly precise, wrong answers." Estimated capture probabilities can be misleadingly high in these situations (White et al. 1982; see Riley et al. [1993] for empirical evidence) and hence should not be relied upon as measures of validity.

A pilot study should be conducted to ensure that a proposed method for estimating abundance is both reasonable, with respect to its assumptions and feasibility, and cost-efficient (Burnham et al.

1987; Thompson et al. 1998; Buckland et al. 2001). Proper validation of an enumeration method requires a known (or nearly so) population of fish to serve as a benchmark for bias evaluation (e.g., use of a known stocked or marked population of fish by Rodgers et al. [1992]). Comparison of two index or untested methods (e.g., snorkel counts versus unverified removal estimates) will only reveal the relative sampling efficiency between the methods. Such a comparison is meaningless if the objective is validation, or evaluation of the magnitude of bias. The usefulness of abundance estimates depends on how closely the estimates approximate reality, not on how closely they approximate each other.

If neither Hankin and Reeves' (1988) approach nor the suggested alternatives are feasible in a given stream, emphasis should be placed on developing alternatives to estimating fish abundance rather than simply defaulting to an existing approach that is known to be inappropriate. Indeed, too often, an existing method is implemented with little thought towards verifying its ability to produce meaningful abundance estimates in the species of interest. I argue that poor abundance estimates may be worse than none at all, because they can lead to incorrect conclusions (e.g., Anderson 2001). Great care and thought must be applied to designing and validating enumeration procedures, because population estimates are only as useful as the data that generated them.

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References

- Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin* 29:1294–1297.
- Anderson, D. R., K. P. Burnham, and G. C. White. 1998. Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture–recapture studies. *Journal of Applied Statistics* 25: 263–282.
- Bayley, P. B. 1993. Quasi-likelihood estimation of marked fish recapture. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2077–2085.
- Bayley, P. B., and D. C. Dowling. 1993. The effect of habitat in biasing fish abundance and species richness estimates when using various sampling methods in streams. *Polish Archives in Hydrobiology* 40:5–14.
- Bohlin, T. 1982. The validity of the removal method for small populations: consequences for electrofishing practice. Institute of Freshwater Research Drottningholm Report 60:15–18.
- Bohlin, T., and B. Sundstrom. 1977. Influence of unequal catchability on population estimates using the Lincoln Index and the removal method applied to electrofishing. *Oikos* 28:123–129.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph No. 5.
- Cochran, W. G. 1977. Sampling techniques, 3rd edition. Wiley, New York.
- Cox, D. R., and E. J. Snell. 1989. Analysis of binary data, 2nd edition. Chapman and Hall, London.
- Dolloff, C. A., J. Kershner, and R. Thurow. 1996. Underwater observation. Pages 533–554 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Ensign, W. E., P. L. Angermeier, and C. A. Dolloff. 1995. Use of line transect methods to estimate abundance of benthic stream fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 52:213–222.
- Hankin, D. G. 1984. Multistage sampling designs in fisheries research: applications in small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1575–1591.
- Hankin, D. G., and G. H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. *Canadian Journal of Fisheries and Aquatic Sciences* 45:834–844.
- Huggins, R. M. 1989. On the statistical analysis of capture experiments. *Biometrika* 76:133–140.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732.
- Johnson, B. K., F. G. Lindsey, and R. J. Guenzel. 1991. Use of aerial line transect surveys to estimate pronghorn populations in Wyoming. *Wildlife Society Bulletin* 19:315–321.
- Kendall, W. L. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. *Ecology* 80:2517–2525.
- Krebs, C. J. 1999. Ecological methodology, 2nd edition.

- Addison Wesley Longman, Inc., Menlo Park, California.
- Laake, J. L., S. T. Buckland, D. R. Anderson, and K. P. Burnham. 1993. DISTANCE user's guide, v. 2.0. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado.
- Manly, B. F. J., L. L. McDonald, and G. W. Garner. 1996. Maximum likelihood estimation for the double-count method with independent observers. *Journal of Agricultural, Biological, and Environmental Statistics* 1:170–189.
- McCullagh, P., and J. A. Nelder. 1989. Generalized linear models, 2nd edition. Chapman and Hall, New York.
- Mesa, M. G., and C. B. Schreck. 1989. Electrofishing mark–recapture and depletion methodologies evoke behavioral and physiological changes in cutthroat trout. *Transactions of the American Fisheries Society* 118:644–658.
- Morisita, M. 1962. Id-index, a measure of dispersion of individuals. *Researches in Population Ecology* 4:1–7.
- Nordwall, F. 1999. Movements of brown trout in a small stream: effects of electrofishing and consequences for population estimates. *North American Journal of Fisheries Management* 19:462–469.
- Northcote, T. G., and D. W. Wilkie. 1963. Underwater census of stream fish populations. *Transactions of the American Fisheries Society* 92:146–151.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monograph* No. 62.
- Peterson, J. T. 2000. Development of interim tools for detecting bull trout detection probabilities. Unpublished final report to Washington Department of Natural Resources, Olympia. Summary available: http://www.uga.edu/~gacoop/peterson/BTR_guides.htm.
- Peterson, N. P., and C. J. Cederholm. 1984. A comparison of the removal and mark–recapture methods of population estimation for juvenile coho salmon in a small stream. *North American Journal of Fisheries Management* 4:99–102.
- Pollock, K. H., J. E. Hines, and J. D. Nichols. 1984. The use of auxiliary variables in capture–recapture and removal experiments. *Biometrics* 40:329–340.
- Reynolds, J. B. 1996. Electrofishing. Pages 221–253 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Riley, S. C., and K. D. Fausch. 1992. Underestimation of trout population size by maximum-likelihood removal estimates in small streams. *North American Journal of Fisheries Management* 12:768–776.
- Riley, S. C., R. L. Haedrich, and R. J. Gibson. 1993. Negative bias in removal estimates of Atlantic salmon parr relative to stream size. *Journal of Freshwater Ecology* 8(2):97–101.
- Rodgers, J. D., M. F. Solazzi, S. L. Johnson, and M. A. Buckman. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. *North American Journal of Fisheries Management* 12:79–86.
- Roper, B. B., and D. L. Scarnecchia. 1995. Observer variability in classifying habitat types in stream surveys. *North American Journal of Fisheries Management* 15:49–53.
- Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in north-central Idaho. *Journal of Wildlife Management* 51:622–630.
- SAS Institute. 2000. SAS language reference: dictionary. Version 8. SAS Institute, Inc., Cary, North Carolina.
- Scheaffer, R. L., W. Mendenhall, and L. Ott. 1990. Elementary survey sampling, 4th edition. PWS-Kent, Boston.
- Smith-Gill, S. J. 1975. Cytophysiological basis of disruptive pigmentary patterns in the leopard frog *Rana pipiens*. II. Wild type and mutant cell specific patterns. *Journal of Morphology* 146:35–54.
- Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. *Biometrics* 45:415–425.
- Swenson, W. A., W. P. Gobin, and T. D. Simonson. 1988. Calibrated mask-bar for underwater measurement of fish. *North American Journal of Fisheries Management* 8:382–385.
- Thomas, L. 1999. DISTANCE 3.5: software for analysis of distance sampling data. *Bulletin of the Ecological Society of America* 80:114–115. Available: <http://www.ruwpa.st-and.ac.uk/distance/distancedownload.html>.
- Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego.
- Wedderburn, R. W. M. 1974. Quasi-likelihood functions, generalized linear models, and the Gauss–Newton method. *Biometrika* 61:439–447.
- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico. Available: <http://www.cnr.colostate.edu/~gwhite/software.html>.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(supplement):S120–S139. Available: <http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>.
- Zippin, C. 1958. The removal method of population estimation. *Journal of Wildlife Management* 22:82–90.