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Change-in-Ratio Estimators for Habitat Usage and Relative Population Size

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SUMMARY

New change-in-ratio methods are developed for estimating the proportion of a population in each of several defined regions. The procedures assume population closure so that an observed decline in catch rate in one region must be balanced by increased catch rates elsewhere. Sampling gear catchability can be unknown and variable among regions. The method was used to estimate the proportion of a population of juvenile striped bass occurring in a river region slated for filling. Formulas are also given for constructing an index of abundance and for estimating the relative efficiencies of the sampling gears in the different regions.

1. Introduction

A given animal population may occur simultaneously in several habitats in proportions that vary over time. If the sampling gears used in the different habitats have unknown relative efficiencies, then it is difficult to assess the relative abundance of animals in the different habitats. Relative abundances may be important information for planners and resource managers seeking rational criteria for siting development projects. Similarly, it is difficult to determine trends in population abundance over time when changes in observed catch rate may be due, at least in part, to changes in geographical distribution.

In this paper, we describe new change-in-ratio estimators for the proportion of the population in each defined region and for the relative population size. The method relies on four assumptions: (1) catch rate is directly proportional to abundance within a region; (2) the efficiencies of the sampling gears remain constant over the course of the study; (3) the population is closed; and (4) the proportion of the population within each region is variable over the course of the study. The closure assumption implies a conservation of numbers so that a decline in catch per unit of effort in one region must be balanced by increases in catch per unit effort elsewhere. In other words, changes in observed catch rates are assumed due to a redistribution of the population among regions. Extensive local movements over short periods of time are rather common in the animal kingdom. This suggests that the method may be widely applicable.

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Stochastic models for change-in-ratio problems were developed by Chapman (1954, 1955), Chapman and Murphy (1965), Paulik and Robson (1969), and Pollock et al. (1985). An extensive review may be found in Seber (1982, Chap. 9). The usual situation is to attribute the change noted in a population's composition to known or estimated removals or additions under the assumption that all types of animals are equally catchable. Pollock et al. (1985) describe a study design that is robust to the assumption of equal catchability. Change-in-ratio theory has been developed extensively over the years. There are now several methods in which information on the composition (instead of magnitude) of the removals or additions is used to estimate exploitation rates, relative survival rates, adult sex ratio, or productivity (relative recruitment) (see Seber, 1982). The method described here differs from previous approaches in that the known selective removal (or relative rate of removal) is replaced with a transformation, of unknown magnitude, of one type of animal to another type, i.e., the transformation consists of a net movement of animals from one region to another. Also, our method allows for an arbitrary number of classes (i.e., regions) in the population and allows one to fix the sampling effort for each class. Previously, Otis (1980) had generalized a change-in-ratio method to allow for three classes in the population.

In Section 2, we illustrate the logic of the methodology by developing moment-type estimators for the simplest case of just two regions. We also use the delta method to derive variances. The approach is generalized to L regions in Section 3. The estimators are shown to be maximum likelihood in many cases. Section 4 describes a case study involving potential impacts of a proposed highway construction project on a striped bass population. The next section describes some small-sample properties and sensitivity to failures of some assumptions. The final section discusses the assumptions and study design.

2. The Two-Region, Two-Sample Case

Suppose a closed population occurs in two distinct and definable regions, such as shallow water and deep water. The catchability of the sampling gear used in one region may possibly differ from that used in the other region. Let $\hat{y}_{ij}$ be the mean catch per unit of sampling effort, estimated according to any appropriate sampling design, in region j at time i, for $i = 1, 2$ and $j = 1, 2$. From assumptions (1) and (2), the expected value of $\hat{y}_{ij}$ is directly proportional to the size N_{ij} of the population present, i.e.,

$$\mathrm{E}(\hat{y}_{ij}) = q_j N_{ij} \equiv y_{ij}. \tag{2.1}$$

The coefficient q_j is commonly referred to as the catchability coefficient. When q_j is small—say, less than .01—it can be interpreted as the proportion of the population present (in the region) which is captured by one unit of sampling effort (Ricker, 1975). Note that the proportionality constants are assumed to be region-specific but constant over the time span of the study. The assumption embodied by equation (2.1) is common in fisheries and wildlife literature (Ricker, 1975; Gulland, 1983; Otis et al., 1978) and is discussed in further detail in Section 5.

Equation (2.1) implies that a given proportional change in population size in a region, c_j, will result in the same proportional change in the expected mean catch per unit of effort. Thus,

$$c_j = \frac{N_{2j} - N_{1j}}{N_{1j}} = \frac{y_{2j} - y_{1j}}{y_{1j}}.$$

An estimate of c_j can be obtained by the method of moments by

$$\hat{c}_j = \frac{\hat{y}_{2j} - \hat{y}_{1j}}{\hat{y}_{1j}}. \tag{2.2}$$

It follows that, if the population is closed [assumption (3)] and the abundance of animals in region 1 declines, then this must be balanced by a gain in region 2. Thus,

$$c_1 N_{11} + c_2 N_{12} = 0. \tag{2.3}$$

Equation (2.3) is easily solved for the ratio of abundances in the two regions at time 1, N_{11}/N_{12}, and hence also for the initial proportion, p_{1j} [$= N_{1j}/(N_{11} + N_{12})$], in each region. Method of moments estimators are

$$\hat{p}_{11} = \frac{\hat{c}_2}{\hat{c}_2 - \hat{c}_1}, \tag{2.4a}$$

$$\hat{p}_{12} = 1 - \hat{p}_{11}. \tag{2.4b}$$

At time 2, the proportion in each region is estimated by

$$\hat{p}_{21} = \hat{p}_{11}(1 + \hat{c}_1), \tag{2.4c}$$

$$\hat{p}_{22} = 1 - \hat{p}_{21}. \tag{2.4d}$$

A consistent index of abundance, i.e., a measure of abundance relative to the (unknown, but fixed) catchability in region j (say), is estimated by

$$\hat{R}^{(j)} = \frac{\hat{y}_{1j}}{\hat{p}_{1j}}. \tag{2.5}$$

A series of estimates of R obtained over several years can be used to look for trends in population abundance. This procedure explicitly accounts for the fact that the distribution of the population among regions may vary from time to time and thus provides a significant advantage over the use of a simple average over space of catch rates.

Finally, it may be of interest to estimate the relative efficiency of the two sampling gears. The proportion of the animals encountering the gear which is retained by the gear (ϕ_j) is related to the catchability coefficient by

$$\phi_j = q_j s_j,$$

where s_j is the size (area or volume) of the jth region relative to the area or volume sampled by the gear. This is because q_j is the proportion of the population captured by one randomly placed unit of sampling effort, while s_j is the reciprocal of the proportion of the population encountered by one random unit of sampling. The relative efficiency of the two gears is the ratio of their probabilities of capture. Thus, from (2.1) and (2.4),

$$\widehat{\left(\frac{\phi_1}{\phi_2}\right)} = \frac{s_1 \hat{q}_1}{s_2 \hat{q}_2} = \frac{s_1 \hat{y}_{11}(1 - \hat{p}_{11})}{s_2 \hat{y}_{12} \hat{p}_{11}} = \frac{s_1(\hat{y}_{11} - \hat{y}_{21})}{s_2(\hat{y}_{22} - \hat{y}_{12})}.$$

The approximate (asymptotic) variances of these estimators are easily found by the Taylor's series or delta method approach (Kendall and Stuart, 1977; Seber, 1982). We assume that each mean catch per unit of effort y_{ij} is estimated independently of the others.

The variances of the initial proportions are given by

$$\begin{aligned} \text{var}(\hat{p}_{1j}) \approx g^{-4}\{&(y_{22} - y_{12})^2 y_{12}^2 y_{21}^2 \text{var}(\hat{y}_{11}) \\ &+ (ay_{21} - gy_{11})^2 \text{var}(\hat{y}_{12}) + (ay_{12})^2 \text{var}(\hat{y}_{21}) + [y_{11}(g - a)]^2 \text{var}(\hat{y}_{22})\}, \end{aligned} \tag{2.6}$$

where

$$a = y_{11}(y_{22} - y_{12}),$$

$$g = y_{11} y_{22} - y_{12} y_{21}.$$

For the second time period,

$$\mathrm{var}(\hat{p}_{2j}) \approx g^{-4}[d^2y_{21}^2y_{22}^2\mathrm{var}(\hat{y}_{11}) + y_{21}^2(dy_{21}-g)^2\mathrm{var}(\hat{y}_{12}) + d^2(g+y_{12}y_{21})^2\mathrm{var}(\hat{y}_{21}) + y_{21}^2(g-dy_{11})^2\mathrm{var}(\hat{y}_{22})],$$

where $d = y_{22} - y_{12}$.

The variance of the estimated index of abundance, $\hat{R}^{(j)}$, when the gear efficiency in region 1 is used as the standard, is

$$\mathrm{var}[\hat{R}^{(1)}] \approx d^{-2}y_{22}^2\mathrm{var}(\hat{y}_{11}) + d^{-2}y_{12}^2\mathrm{var}(\hat{y}_{21}) + d^{-4}e^2y_{22}^2\mathrm{var}(\hat{y}_{12}) + d^{-4}(ey_{12})^2\mathrm{var}(\hat{y}_{22}),$$

where $e = y_{21} - y_{11}$.

Finally, the variance of the estimated ratio of gear efficiencies, when the sizes s_j of the regions are assumed known constants, is

$$\mathrm{var}\widehat{\left(\frac{\phi_1}{\phi_2}\right)} \approx \frac{s_1^2}{s_2^2}\{d^{-2}[\mathrm{var}(\hat{y}_{11}) + \mathrm{var}(\hat{y}_{21})] + e^2d^{-4}[\mathrm{var}(\hat{y}_{12}) + \mathrm{var}(\hat{y}_{22})]\}.$$

3. The *L*-Region, *L*-Sample Case

Suppose the study area has been divided into L regions that have been sampled on L occasions. The expected value of the catch per unit of effort in region j at time i is given by

$$\mathrm{E}(\hat{y}_{ij}) = y_{ij} = p_{ij}q_jN, \tag{3.1}$$

where p_{ij} is the proportion of the population found in region j at time i, q_j is the catchability coefficient in region j, and N is the total population size.

The proportion of the stock summed over all regions at any time must equal unity, so

$$\mathbf{P1} = \mathbf{1} = \mathbf{Yb}, \tag{3.2}$$

where $\mathbf{P}$ is the $L \times L$ matrix with elements $[p_{ij}]$, $\mathbf{1}$ is the $L \times 1$ unit vector, $\mathbf{Y}$ is the $L \times L$ matrix with elements $[y_{ij}]$, and $\mathbf{b}$ is the $L \times 1$ vector with elements $b_j = [(q_jN)^{-1}]$.

It follows from (3.2) and (3.1) that

$$\mathbf{b} = \mathbf{Y}^{-1}\mathbf{1}$$

and

$$\mathbf{P} = \mathbf{Y}\ \mathrm{diag}\ \mathbf{b} = \mathbf{Y}\ \mathrm{diag}[\mathbf{Y}^{-1}\mathbf{1}], \tag{3.3}$$

assuming the matrix $\mathbf{Y}$ is not singular. An estimate of $\mathbf{P}$ is obtained by the method of moments by substituting the estimates $\hat{\mathbf{Y}}$ for $\mathbf{Y}$.

The ratio of the gear efficiency in region i to that in region j is found from the definition of $\mathbf{b}$ to be

$$\frac{\phi_i}{\phi_j} = \frac{b_js_i}{b_is_j}.$$

Again, an estimate of this ratio is obtained by substituting the sample estimates for the values of b_i and b_j.

The asymptotic variances and covariances for these estimators are presented in the Appendix.

In many, if not most, applications, the estimates $\hat{y}_{ij}$ will be the maximum likelihood estimates for the mean catch rates. For example, if the catch per tow is assumed normally distributed, and $\hat{y}_{ij}$ is the sample mean from a simple random sampling scheme, then $\hat{y}_{ij}$ is of maximum likelihood. In this case, the estimates of the relative gear efficiencies and of the p_{ij} will be one-to-one functions of maximum likelihood estimates (assuming $\hat{\mathbf{Y}}$ nonsingular), and thus will themselves be of maximum likelihood by the invariance principle provided, of course, that the estimates are feasible (in the interval from 0 to 1). Furthermore, the covariance matrix obtained by the delta method is the same as that obtained by inverting the information matrix if the distributions of catch per tow are in the exponential family (Brownie et al., 1985; Burnham, personal communication).

4. Example: Striped Bass and the Westway Highway

This example concerns the potential impact of the Westway Highway construction project in New York City on the overwintering population of young-of-the-year and yearling striped bass (*Morone saxatilis*) in the Hudson River. Controversy arose over the importance to the population of the more than 200 acres of shallow area that were slated to be filled. This controversy led to a series of lengthy legal proceedings that were summarized by Moran and Kieffer (1986).

The simplest approach to evaluating the proportion of the population in the project area would be to estimate the ratio of the relative abundance in the project area to the relative abundance in the entire river (where relative abundance is computed as an aerial expansion of the mean catch per unit area sampled). This was deemed inappropriate because the project area consisted of shallow interpier basins, which necessitated making modifications to the sampling procedure used in open water areas. It was suspected that the catchability coefficient in the interpier basins was much smaller than in open water areas. If so, the estimated proportion of the population in the shallow area would tend to be too low.

The change-in-ratio method described here was developed by the first author (Martin Marietta Environmental Systems, 1984) to estimate the proportion of the population of young bass in the Westway project area. The data presented were collected in 1984 as part of the U.S. Army Corps of Engineers, New York District, Westway Fisheries Study.

The entire known winter geographic distribution of young Hudson River striped bass was sampled periodically from December 1983 through April 1984. Sampling was conducted according to a stratified random sampling design in which 24 strata were defined by geographic location and water depth. At least three replicate samples were taken in each stratum at randomly selected locations. Sampling of the entire study area required 10 days, and 11 contiguous 10-day sampling periods comprised the study.

The sampling unit was a 3-minute tow made with a 30-foot flat otter trawl. The variable of interest was the number of young-of-the-year (1983 year class) striped bass caught, and this was taken to be equal to the number of fish in the trawl measuring less than 150 mm.

As described in the discussion (Section 6), it was desirable to analyze data from short study intervals. Consequently, sampling strata were aggregated into three regions to allow analysis of data from 30-day intervals (i.e., three consecutive, 10-day periods). Estimates of mean catch per unit effort and associated variance estimates from one 30-day interval are presented in Table 1. These estimates refer to the following three geographic regions (see Figure 1):

Region 1: Peekskill South to Tarrytown;

Region 2: Tarrytown South to the Verrazano Narrows, including Newark Bay and the East River, but excluding the interpier areas on the Manhattan shoreline of the Hudson River between the George Washington Bridge and the Battery;

Region 3: Interpier areas on the Manhattan shoreline of the Hudson River between the George Washington Bridge and the Battery. (The southern portion of this region encompassed the Westway project area.)

Table 1
Estimates of mean catch per unit of sampling effort ($\hat{y}$) of young-of-the-year striped bass in the Hudson River and adjacent waterways in 1984, with estimates of corresponding variances (see text and Fig. 1 for definitions of regions)

		Region					
		1		2		3	
Time period	Dates	$\hat{y}$	$\text{var}_{\text{est}}(\hat{y})$	$\hat{y}$	$\text{var}_{\text{est}}(\hat{y})$	$\hat{y}$	$\text{var}_{\text{est}}(\hat{y})$
1	22 March–31 March	2.04	.55	17.89	13.25	6.80	2.44
2	1 April–10 April	10.62	9.66	11.44	8.46	6.93	3.95
3	11 April–20 April	5.89	1.38	4.16	.25	16.87	9.59

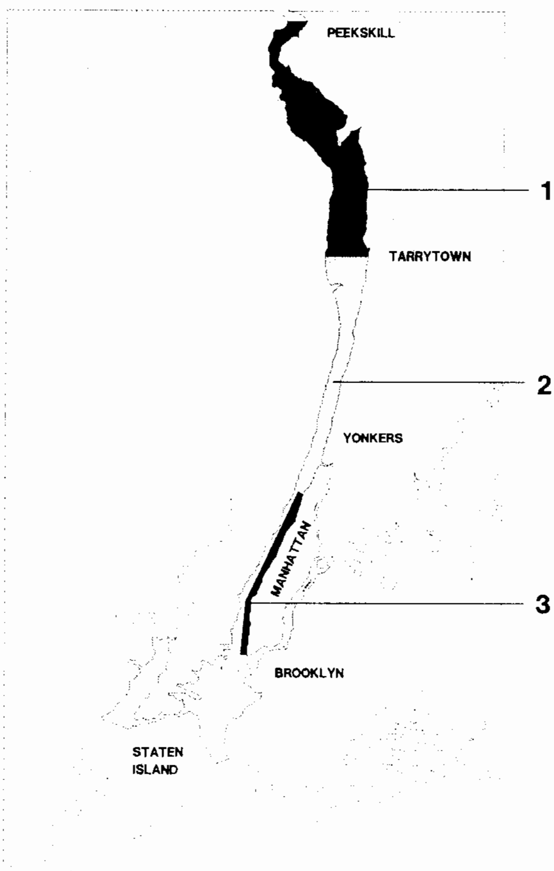

Figure 1. Map of the Hudson River and adjacent waterways showing the entire known geographical distribution of young-of-the-year Hudson River striped bass in winter. Shadings indicate the three regions defined in the analysis.

Estimates were computed of the proportion of the population in each of these regions at each of the three times using (3.3) (see Table 2). The variances were computed using (A.2). These results, in conjunction with analytical results for the rest of the data collected, suggest that the Hudson River shallow areas along Manhattan Island may have harbored a substantial portion of the overwintering population of the 1983 year class of Hudson River striped bass.

To test whether the results are highly dependent on the assumption of no mortality, we conducted a sensitivity analysis in which a 10% mortality rate was assumed between sampling times. This mortality rate is believed to be conservative on the basis of comparison with literature values [i.e., 5% in Dey (1981) and 11% in Saila and Lorda (1977)]. The adjustment of the catch rates for mortality results in slightly lower estimates of the proportions in regions 1 and 3 and higher estimates in region 2 (Table 3). However, the overall conclusions do not change much when the catch rates are adjusted.

Table 2

Estimates of the proportion ($\hat{p}$) of the young-of-the-year striped bass in each of 3 regions in 3 successive time periods in 1984, and corresponding standard error estimates (see text and Fig. 1 for description of the regions)

		Region					
		1		2		3	
Time period	Dates	$\hat{p}$	se($\hat{p}$)	$\hat{p}$	se($\hat{p}$)	$\hat{p}$	se($\hat{p}$)
1	22 March–31 March	.06	.0510	.67	.0938	.27	.0989
2	1 April–10 April	.29	.2090	.43	.1533	.28	.1300
3	11 April–20 April	.16	.1349	.16	.0458	.68	.1285

Table 3

Sensitivity analysis for striped bass example. Second-period catch rates in Table 1 were divided by .9 to account for a 10% mortality; third-period catch rates were divided by .81 (= .9²). Table gives adjusted estimates ($\hat{p}$) of the proportion in each region at each time and the difference in computed results ($p^* - \hat{p}$).*

	Region					
	1		2		3	
Time period	p^*	$p^* - \hat{p}$	p^*	$p^* - \hat{p}$	p^*	$p^* - \hat{p}$
1	.04	−.02	.75	.08	.21	−.06
2	.23	−.06	.53	.10	.24	−.04
3	.14	−.02	.22	.06	.64	−.04

5. Small-Sample Properties and Sensitivity Analysis

Small-sample properties of the change-in-ratio estimator were examined by Monte Carlo simulation. We assumed that for the two-region, two-sample case, the distribution of the estimated mean catch per unit of sampling effort was normally distributed as follows:

$$\hat{y}_{i1} \sim \mathrm{N}(q_1 N p_{i1},\ v q_1 N p_{i1}),$$

$$\hat{y}_{i2} \sim \mathrm{N}(q_1 N (q_2/q_1) p_{i2},\ v q_1 N (q_2/q_1) p_{i2}),$$

for $i = 1, 2$, where q_2/q_1 is the ratio of catchability in region 2 to that in region 1, and v is a constant relating the variance to the mean. Thus, it is assumed that the sampling intensity in each region is such that the variances are some fixed fraction v of the means. Note that the value of $q_1 N$ does not affect the estimation procedure and can therefore be set equal to an arbitrary value. We simulated data sets with various combinations of the parameters p_{11}, p_{21}, q_2/q_1, and v.

Figure 2 contains contours showing the precision (as measured by v) necessary to ensure that the probability of obtaining unfeasible results is less than 5%. Except when the change

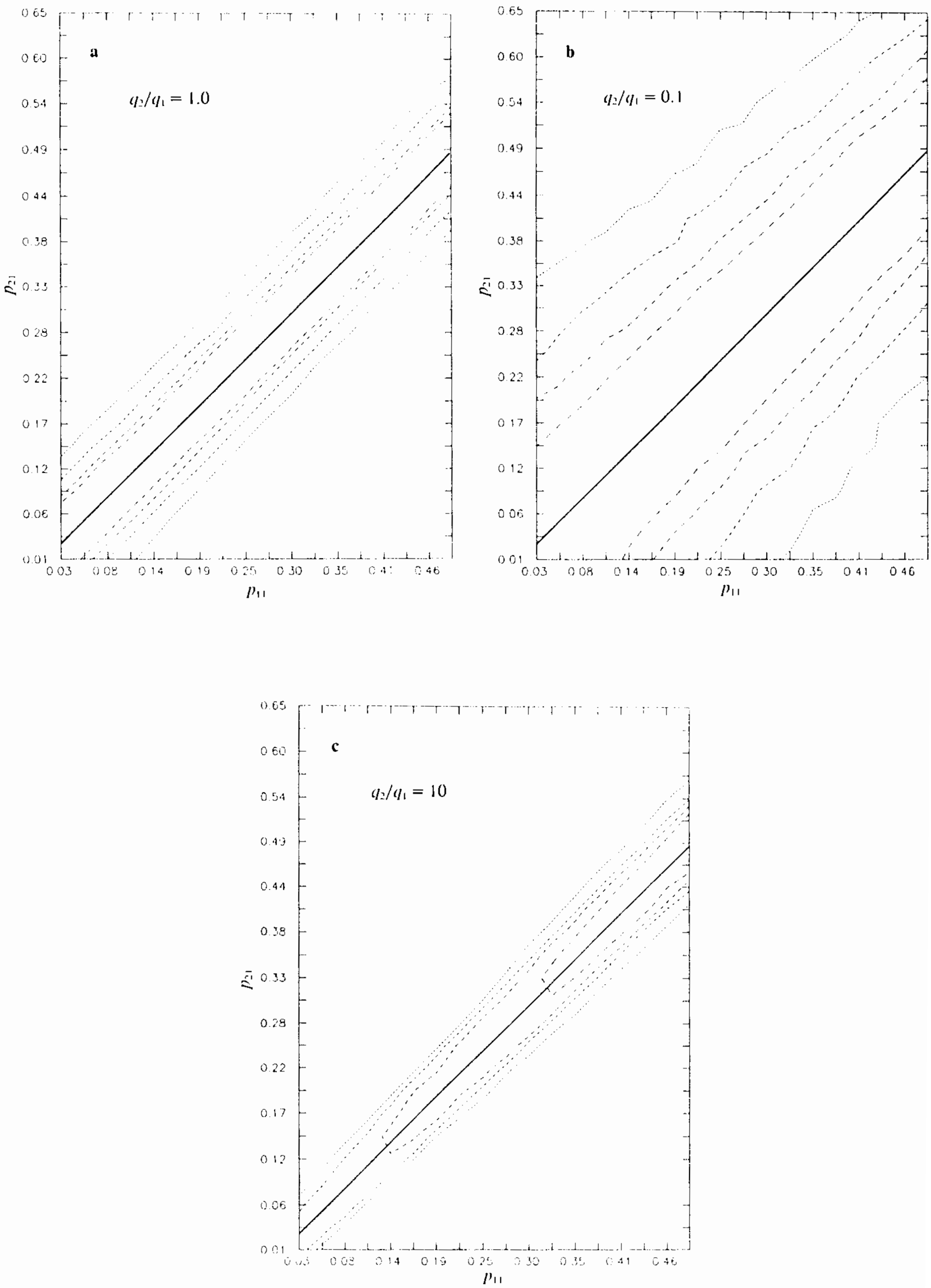

Figure 2. Contours showing precision (v, the coefficient relating the variance to the mean) necessary to have a 5% chance of obtaining unfeasible results. From outermost to innermost pair, contours represent v = .2, .10, .05, and .025. Solid line indicates where $p_{11} = p_{21}$. **(a)** $q_2/q_1 = 1.0$; **(b)** $q_2/q_1 = .1$; **(c)** $q_2/q_1 = 10$.

in the proportion in region 1 is small, the chances of obtaining unfeasible results are small if $q_1 = q_2$ (Fig. 2a). For example, when the variances are one-fifth of the means, the value of the proportion in region 1 must change by .10 (absolute magnitude) in order to have less than a 5% chance of obtaining unfeasible results. When q_2/q_1 is less than unity and p_{11} is less than .5, a larger change in proportions is needed to keep the probability of unfeasible results under 5% (Figure 2b) compared to when q_2/q_1 equals unity. Conversely, when q_2/q_1 is greater than unity and p_{11} is less than .5, a smaller change in proportions is sufficient to keep the probability of obtaining unfeasible results low.

The Monte Carlo simulation also indicated that the bias is 10% or less when the sampling precision v is sufficient to ensure a probability less than 5% of obtaining unfeasible results. Also, the asymptotic variance formula (2.6) was within 50% of the true (observed) variance when the proportion of unfeasible results was under 5%.

The effects of failures of assumptions were investigated by sensitivity analysis. Mortality, immigration, emigration, and recruitment all influence the estimation procedure by affecting catch rates. Consider the effects of a 10% mortality occurring between sampling times 1 and 2. The expected catch rates at time 2 would be reduced by 10%:

$$y_{21}^* = .9q_1Np_{21},$$

$$y_{22}^* = .9q_1N(q_2/q_1)(1 - p_{21}),$$

where the asterisk indicates the occurrence of mortality.

In Figure 3 are shown the effects of computing estimates of p_{11} from the expected catches when the values at time 2 are 10% too low. The results do not depend on the values chosen

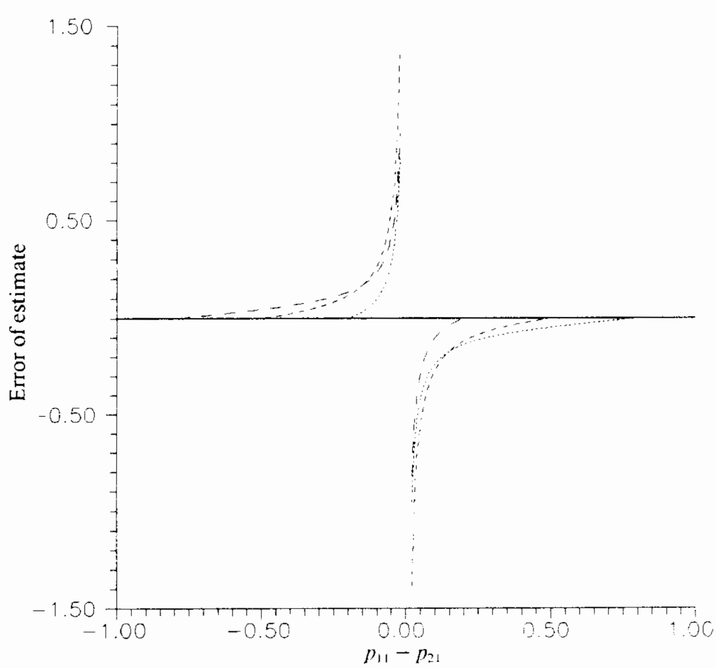

Figure 3. Sensitivity analysis of the two-region, two-sample case showing the effects of a 10% loss to the population (mortality) between sampling times 1 and 2 on the computed value of p_{11}. Ordinate is erroneous estimate minus true value; axis is change in proportion of population in region 1 between times 1 and 2. Short dashes represent case where $p_{21} = .2$; medium dashes, $p_{21} = .5$; long dashes, $p_{21} = .8$.

for q_1N or q_2/q_1. The critical factor appears to be the amount by which the proportion in region 1 changes between sampling times. When this change is large, the procedure is robust to the assumption of no mortality. When the change is very small, the procedure is sensitive to mortality.

6. Discussion

6.1 *Failures of Assumptions*

The four assumptions of the method may seem quite restrictive but they can often be met by careful choice of the study design. The types of possible failure, and ways for minimizing their impact, are discussed below.

Population closure implies no recruitment, mortality, immigration, or emigration. By choosing a suitably short study period, the amount of mortality and recruitment can be kept small. Migration should not be a problem if the study is conducted in a closed system such as a lake, or if the entire range of the population can be sampled, as in the Westway case.

The assumption that catch rate is proportional to abundance within a region can fail in four ways: by temporal variation, according to behavioral responses, due to population heterogeneity, and according to animal density (Otis et al., 1978; Gulland, 1983). Temporal variation in catch rates (e.g., due to changing weather conditions) can be minimized when the study period is kept short. Behavioral responses (e.g., "trap-happy" or "trap-shy" animals) can be a problem when the probability of capture is high enough that multiple encounters with the sampling gear are likely. This is most likely to occur when the study regions are defined over small geographical areas with small populations. Population heterogeneity refers to the situation where different segments of the population under study have different probabilities of capture. The change-in-ratio method allows for heterogeneity among regions. Within-region heterogeneity can be minimized by defining the study population as homogeneously as possible. For example, in the Westway study the young-of-the-year striped bass population was studied separately from the yearling population to minimize heterogeneity due to size and age. Finally, the catchability of the population in a given region may vary as a function of the size of the population present due to factors such as gear saturation. This can be minimized by using short net tows or trap sets so that saturation is not significant.

The proportion of the population in each region must be variable over the course of the study since it is the net movements among regions that allow one to estimate the proportions. Mathematically, the inverse of the catch matrix $\hat{\mathbf{Y}}$ must exist in order to use the estimators presented here. This suggests that the determinant of $\hat{\mathbf{Y}}$ should be useful for evaluating the validity of the assumption. In the Westway study, estimates of $\mathbf{P}$ were considered unreliable if the ratio of the standard error of the determinant of $\hat{\mathbf{Y}}$ to the determinant of $\hat{\mathbf{Y}}$ was large.

The constancy of the relative efficiencies of the sampling gears is best achieved if the duration of the study is kept short (to minimize environmental changes) and if short net tows or trap sets are employed (to minimize gear saturation problems).

6.2 *Study Design*

The above considerations suggest strongly that the duration of the study be kept short in order to minimize the likelihood of failures of the assumptions. One way to do this is to define and sample many subregions and then aggregate these subregions in various ways for purposes of analysis. That is, different aggregations of the same data can be used to obtain a variety of estimates. For example, one may sample 10 subregions on each of three occasions. The data from these 10 regions can then be aggregated in various ways into three regions (which comprise the entire study region), and each set of three regions can then be used to produce estimates of the proportions. Experience gained from the Westway study suggests that the chances of obtaining feasible estimates with reasonable standard errors are increased when the number of regions and times analyzed (L) is kept small.

As a practical matter, it is necessary to sample on more occasions than there are defined regions in order to be assured of obtaining at least one subset of the data in which the necessary net movements among regions have occurred. This usually provides for a number of possible estimates of the population proportions which can be used to judge the reliability of the results. This approach was used in the Westway study.

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Résumé

De nouvelles méthodes de modification du rapport sont développées pour estimer la proportion de la population dans plusieurs régions prédéfinies. La procédure suppose l'isolement de la population, de façon que l'observation d'un déclin du taux de captures dans une région puisse être contrebalancée par son accroissement dans une autre. La méthode a été utilisée pour estimer la proportion de bars à bandes juvéniles d'une population de *Morone saxatilis* présente dans une portion de rivière délimitée pour le remplissage. Des formules sont données également pour construire un index d'abondance et pour estimer l'efficacité relative des tournées d'échantillonnage dans les différentes régions.

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APPENDIX

To find the covariance matrix for $\hat{\mathbf{P}}$, it is convenient to work with (3.3) in the form

$$p_{ij} = y_{ij} b_j = y_{ij} \sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{jh} = g_{ij}(\mathbf{Y}) \quad \text{(say)},$$

where $[\mathbf{Y}^{-1}]_{jh}$ is the jhth element of $\mathbf{Y}^{-1}$. The delta or Taylor's series method is used to obtain

$$\text{var}(\hat{p}_{ij}) \approx \sum_{m=1}^{L} \sum_{n=1}^{L} \left\{ \frac{\partial g_{ij}}{\partial y_{mn}} \right\}^2 \text{var}(\hat{y}_{mn}) \tag{A.1}$$

(again assuming that all y_{ij} are estimated independently). The partial derivatives of a matrix $\mathbf{X}^{-1}$ with respect to the ijth element of $\mathbf{X}$ are given by (Morrison, 1976)

$$\frac{\partial \mathbf{X}^{-1}}{\partial x_{ij}} = -\mathbf{X}^{-1} \mathbf{J}_{ij} \mathbf{X}^{-1},$$

where $\mathbf{J}_{ij}$ is a matrix with a 1 in the ijth position and 0 elsewhere. Thus,

$$\frac{\partial [\mathbf{X}^{-1}]_{mn}}{\partial x_{ij}} = -[\mathbf{X}^{-1}]_{mi} [\mathbf{X}^{-1}]_{jn}.$$

Substituting into (A.1) gives

$$\text{var}(\hat{p}_{ij}) \approx y_{ij}^2 \sum_{m=1}^{L} \sum_{n=1}^{L} \left\{ [\mathbf{Y}^{-1}]_{jm} \sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{nh} \right\}^2 \text{var}(\hat{y}_{mn})$$

$$+ \left\{ \sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{jh} \right\}^2 \{1 - 2 y_{ij} [\mathbf{Y}^{-1}]_{ji}\} \text{var}(\hat{y}_{ij}). \tag{A.2}$$

The covariance of $\hat{p}_{ij}$ and $\hat{p}_{ik}$ can also be found using the delta method as

$$\text{cov}(\hat{p}_{ij}, \hat{p}_{ik}) \approx \sum_{m=1}^{L} \sum_{n=1}^{L} \left\{ \frac{\partial g_{ij}}{\partial y_{mn}} \right\} \left\{ \frac{\partial g_{ik}}{\partial y_{mn}} \right\} \text{var}(\hat{y}_{mn})$$

$$= y_{ij} y_{ik} \sum_{m=1}^{L} \sum_{n=1}^{L} [\mathbf{Y}^{-1}]_{jm} [\mathbf{Y}^{-1}]_{km} \left(\sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{nh} \right)^2 \text{var}(\hat{y}_{mn})$$

$$- y_{ik} [\mathbf{Y}^{-1}]_{ki} \left(\sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{jh} \right)^2 \text{var}(\hat{y}_{ij})$$

$$- y_{ij} [\mathbf{Y}^{-1}]_{ji} \left(\sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{kh} \right)^2 \text{var}(\hat{y}_{ik}).$$

The asymptotic variance of the estimated ratio of gear efficiencies is

$$\widehat{\operatorname{var}\left(\frac{\phi_i}{\phi_j}\right)} \approx s_i^2 s_j^{-2} \left(\sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{ih} \right)^{-4}$$

$$\cdot \sum_{m=1}^{L} \sum_{n=1}^{L} \left(\sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{nh} \right)^2 \left([\mathbf{Y}^{-1}]_{im} \sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{jh} - [\mathbf{Y}^{-1}]_{jm} \sum_{h=1}^{L} [\mathbf{Y}^{-1}]_{ih} \right)^2 \operatorname{var}(\hat{y}_{mn}).$$