Change-in-Ratio and Index-Removal Methods for Population Assessment and Their Application to Snow Crab (*Chionoecetes opilio*)

Earl G. Dawe, John M. Hoenig, and Xucai Xu

Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St John's, NF AIC 5X1, Canada

Dawe, E.G., J.M. Hoenig, and X. Xu. 1993. Change-in-ratio and index-removal methods for population assessment and their application to snow crab (*Chionoecetes opilio*). Can. J. Fish. Aquat. Sci. 50: 1467–1476.

Change-in-ratio and index-removal estimators are presented in a general form suitable for fisheries studies of closed populations. We also show how to combine the two approaches in a single estimator. In order to use these methods, it is necessary to sample the population before and after the fishery and to determine the total harvest and its composition. We used the methods to estimate the population of legal-size snow crab (*Chionoecetes opilio*) in St. Mary's Bay, Newfoundland, before and after the fishery and to estimate the catchability coefficient and exploitation rate. It is also possible to estimate the abundance of prerecruits but this requires the assumption of equal catchability of all animals, a condition that may not be met. These methods have been largely neglected by fishery scientists; however, they seem to be ideally suited for studies of many temperate populations of large sedentary crustaceans, particularly those subjected to fisheries of short duration.

Des estimateurs des changements dans les proportions et le prélèvement sont présentés sous une forme générale qui se prête aux études d'halieutique de populations fermées. Nous montrons aussi comment combiner les deux approches en un estimateur unique. Afin d'utiliser ces méthodes, il est nécessaire d'échantillonner la population avant et après la pêche, et de déterminer la récolte totale ainsi que sa composition. Nous avons appliqué ces méthodes à l'estimation de la population du crabe des neiges de taille légale (*Chionoecetes opilio*) dans la baie St. Mary's, Terre-Neuve, avant et après la pêche, et nous les avons appliquées à l'estimation du coefficient du potentiel de capture ainsi que du taux d'exploitation. Il est également possible d'estimer l'abondance des jeunes qui ne sont pas encore recrutés, mais pour cela, il faut adopter l'hypothèse selon laquelle tous les sujets sont également sujets à être capturés, ce qui peut se révéler inexact. Ces méthodes ont été largement négligées par les spécialistes des pêches; toutefois, elles semblent convenir parfaitement aux études de bon nombre de populations en zone tempérée de gros crustacés sédentaires, particulièrement ceux qui font l'objet d'une pêche de courte durée.

Received August 27, 1992
Accepted January 28, 1993
(JB608)

Reçu le 27 août 1992
Accepté le 28 janvier 1993

The change-in-ratio method can be used to estimate the size of a closed population when the population can be divided into two classes and when the ratio of these classes changes due to a selective removal from the population. The classification might be based on sex, size, age, maturity status, etc. The method was developed in the 1940s for wildlife studies (Kelker 1940) and has been reviewed by Ricker (1975), Seber (1982), and Pollock (1991). However, to our knowledge, only Murphy (1952) and Chapman (1964) have used variants of the method for fishery problems although Lander (1962), Rupp (1966), and Paulik and Robson (1969) have suggested its use for fisheries studies.

Only male snow crab (*Chionoecetes opilio*) with carapace width greater than or equal to 95 mm may be harvested legally in Atlantic Canada. The fishing season is generally short and often occurs after most of the annual molting and subsequent recruitment have taken place (Miller and O'Keefe 1981). It appears from tagging studies that snow crab do not move great distances so that populations tend to be discrete (Taylor 1992). These observations suggest that change-in-ratio estimation based on sublegal and legal size classes might be effective for estimating the population size and, thus, the exploitation rate and catchability coefficient. This requires research sampling before and after the fishing season and sampling of the commercial fishery to estimate the proportion in each size class. Such sampling would also enable one to use the change in catch rate due to a known removal to provide an alternative method for estimating population parameters. This approach is known as an index-removal estimator (Petrides 1949; Davis 1963; Eberhardt 1982).

In this paper, we explore the use of change-in-ratio and index-removal estimators for snow crab populations. We present the methods in a general form and derive several new variance estimators as well as a new population estimator that combines the change-in-ratio and index-removal methods. Symbols used in the text and appendix are summarized in Table 1. We apply these methods to snow crab data from St. Mary's Bay, Newfoundland.

Materials and Methods

Data Collection and Summarization

Research sampling surveys using Japanese-style, conical, baited traps were carried out in St. Mary's Bay before the snow

TABLE 1. Definition of symbols used in the paper.

Symbol	Definition
$\hat{P}_j$	Estimate of the proportion of x-type animals in the jth survey
$\hat{c}_j$, $\hat{c}_{xj}$	Estimates of catch rates for total and x-type animals, respectively, in the jth survey
z_{ij}, x_{ij}	Numbers of total and x-type animals, respectively, caught in the ith set of the jth survey
n_j	Number of sets in the jth survey
$\bar{z}_j$	Mean number of animals caught per set in the jth survey
$\hat{f}$	Estimate of the proportion of x-type animals landed in the fishery
z^*_m, x^*_m	Numbers of total and x-type animals, respectively, in the mth plant sample
M	Number of plant samples
$\bar{z}^*$, $\bar{x}^*$	Mean number of animals and mean number of x-type animals, respectively, per plant sample
L	Total catch or landing in weight by the fishery
W_{mk}	Weight of the kth crab in the mth plant sample
$\bar{W}$	Mean weight of individual crab landed
$\hat{R}$, $\hat{R}_x$	Estimates of numbers of total and x-type animals, respectively, removed by the fishery
$\hat{N}_1$, $\hat{N}_2$	Estimates of the total population size (x- and y-type animals) before and after the fishery, respectively
$\hat{X}_1$, $\hat{X}_2$	Estimates of the number of x-type animals in the population before and after the fishery, respectively
$\hat{X}_{cir}$, $\hat{X}_{ir}$	Change-in-ratio and index-removal estimators, respectively, of the number of x-type animals in the population before the fishery
$\hat{X}_{com}$	Combined estimator (from change-in-ratio and index-removal estimators) of the number of x-type animals in the population before the fishery
ω	A constant weighting factor used in the combined estimator
$\hat{u}$, $\hat{u}_x$	Estimates of exploitation rates for the total population and for x-type animals, respectively
$\hat{q}$, $\tilde{q}$	Estimates of catchability coefficient for the total population
$\hat{q}_x$	Estimate of catchability coefficient for x-type animals
$E(h)$	Expected catch or harvest from one unit of sampling effort
ρ	Proportion of animals encountering the sampling gear that are retained
a	Area fished by the sampling gear
ϕ	Density of animals (number per unit area)
A	Area encompassed by the stock
Var[·], Covar[·]	True variance and covariance of the estimates
$\hat{V}$[·], Côv[·]	Estimated variance and covariance of the estimates

crab fishery (August 23 – September 2, 1991) and after the fishery (October 21 – October 31, 1991). Two small-mesh traps (25-mm stretched mesh) and four large-mesh traps (133-mm stretched mesh) were used in each set. The large-mesh traps are the same type as used in the commercial fishery. The survey before and after the fishery had 40 and 41 sets, respectively; sampling sites were chosen randomly in that part of the bay deeper than 40 m.

The commercial fishery began on September 2 and ended on September 7. Eighteen plant samples were collected on September 3, 4, and 5 during the fishing season. We treat these samples as randomly selected cluster samples (see Appendix for a discussion of the plant sampling). The carapace width (CW) of each sampled crab was measured to the nearest millimetre. Weights of individual crab were obtained from the regression models of Taylor and Warren (1991) relating weight to carapace width.

The population of male snow crab was divided into two classes defined by the legal size limit of 95 mm CW. Crab greater than or equal to 95 mm CW were designated as x-type and crab greater than or equal to 78 mm but smaller than 95 mm CW were y-type. Any crab less than 78 mm CW were disregarded completely to minimize any effects of size-related variation in catchability. Most of the y-type crab should attain legal size after one more molts and can thus be considered immediate prerecruits (Dawe et al. 1992). The proportion of x-type or legal-size crab in survey j ($j = 1, 2$), P_j, was estimated separately for each trap type by

$$(1) \qquad \hat{P}_j = \frac{\sum_{i=1}^{n_j} x_{ij}}{\sum_{i=1}^{n_j} z_{ij}}$$

where the symbol ^ indicates an estimate and x_{ij} and z_{ij} are the number of x-type crab and the total number of crab ($\geq$ 78 mm CW) caught in the ith set ($i = 1, 2, \ldots n_j$), respectively. Note that the numerator and the denominator in equation (1) are random variables because the number of crab caught is not fixed by the investigator. Thus, equation (1) is a ratio estimator and the variance of $\hat{P}_j$ can be estimated by (see Cochran 1977, p. 66)

$$(2) \qquad \hat{V}[\hat{P}_j] = \frac{\sum_{i=1}^{n_j} (x_{ij} - \hat{P}_j z_{ij})^2}{n_j (n_j - 1) \bar{z}_j^2}$$

where

$$\bar{z}_j = \frac{\sum_{i=1}^{n_j} z_{ij}}{n_j}.$$

The catch rate for x-type crab for survey j ($j = 1, 2$) is estimated by

$$(3) \qquad \hat{c}_{xj} = \frac{1}{n_j} \sum_{i=1}^{n_j} x_{ij}$$

with the variance estimated in the usual way by

$$(4) \qquad \hat{V}[\hat{c}_{xj}] = \frac{\sum_{i=1}^{n_j} (x_{ij} - \hat{c}_{xj})^2}{n_j (n_j - 1)}$$

where x_{ij} is the same as in equation (1).

It is necessary to estimate the proportion of x-type (legal-size) crab in the commercial catch because a small proportion of the catch is represented by illegally landed smaller crab. The estimated proportion, $\hat{f}$, can be obtained from the plant sampling data by using a ratio estimator analogous to equation (1):

$$(5) \qquad \hat{f} = \frac{\sum_{m=1}^{M} x_m^*}{\sum_{m=1}^{M} z_m^*}$$

where x_m^* and z_m^* are the number of x-type crab and the total number of crab in the mth plant sample, respectively, and M is the total number of plant samples ($M = 18$). The variance of $\hat{f}$ is estimated by a formula analogous to equation (2):

$$(6) \qquad \hat{V}[\hat{f}] = \frac{\sum_{m=1}^{M} (x_m^* - \hat{f} z_m^*)^2}{M(M - 1) \bar{z}^{*2}}$$

where $\bar{z}^*$ is the mean of the M values of z_m^*.

The total number of snow crab removed during the fishing season, R, was estimated by

$$(7) \qquad \hat{R} = \frac{L}{\bar{W}}$$

where L is the total catch in weight (assumed known exactly from the purchase records) and $\bar{W}$ is the mean weight of individual crab estimated from the plant sampling,

$$(8) \qquad \bar{W} = \frac{\sum_{m=1}^{M} \sum_{k=1}^{z_m^*} W_{mk}}{\sum_{m=1}^{M} z_m^*}$$

where W_{mk} is the weight of the kth crab in the mth plant sample.

Throughout this paper, we frequently use the delta (or Taylor's series) method to derive asymptotically valid approximations to the variances and covariances of functions of random variables (see Seber 1982, p. 7–9). Let $g(\hat{Y})$ and $h(\hat{Y})$ be functions of the random variables $\hat{Y} = [\hat{Y}_1, \hat{Y}_2, \ldots \hat{Y}_p]$. Then the estimated covariance can be approximated as

$$\hat{\text{Cov}}\,[g(\hat{Y}), h(\hat{Y})] = \sum_{i=1}^{P} \sum_{j=1}^{P} \frac{\partial g}{\partial \hat{Y}_i} \frac{\partial h}{\partial \hat{Y}_j} \hat{\text{Cov}}\,[\hat{Y}_i, \hat{Y}_j] .$$

Note that this formula can also be used to find an estimator of the approximate variance of a function of random variables, since $\hat{\text{Cov}}[g(\hat{Y}), g(\hat{Y})] = \hat{V}[g(\hat{Y})]$.

The estimated variance of $\hat{R}$ (equation (7)) was obtained by the delta method as

$$(9) \qquad \hat{V}[\hat{R}] = \frac{L^2}{\bar{W}^4} \hat{V}[\bar{W}] .$$

Further discussion of the estimation of mean weight and its variance is given in the Appendix.

The number of x-type crab removed during the fishing season, R_x, was estimated by

$$(10) \qquad \hat{R}_x = \hat{f} \hat{R}$$

with the estimated variance obtained by the delta method (see Appendix).

Change-in-Ratio-Method

The proportion of snow crab that are of legal size before the fishery, P_1, is

$$P_1 = \frac{X_1}{N_1}$$

where X_1 and N_1 are the population sizes of x-type crab and total population before the fishery, respectively. The fishery serves to reduce both the number of legal-size crab (numerator) and the total number of crab (denominator). Thus, the proportion that are of legal size after the fishery, P_2, is (see Seber 1982, p. 354)

$$P_2 = \frac{X_1 - R_x}{N_1 - R} = \frac{P_1 N_1 - R_x}{N_1 - R} .$$

Consequently, the population size (in number) before the fishing season, N_1, and the number of legal-size or x-type crab before the fishing season, X_1, can be estimated by

$$(11) \qquad \hat{N}_1 = \frac{\hat{R}_x - \hat{P}_2 \hat{R}}{\hat{P}_1 - \hat{P}_2}$$

$$(12) \qquad \hat{X}_1 = \hat{P}_1 \hat{N}_1.$$

The variance of $\hat{N}_1$ is obtained using the delta method

$$(13) \qquad \hat{V}[\hat{N}_1] = (\hat{P}_1 - \hat{P}_2)^{-2} \{\hat{N}_1^2 \hat{V}[\hat{P}_1] + \hat{N}_2^2 \hat{V}[\hat{P}_2] + \hat{R}^2 \hat{V}[\hat{f}] + (\hat{f} - \hat{P}_2)^2 \hat{V}[\hat{R}] + 2\hat{R}(\hat{f} - \hat{P}_2)\, \hat{\text{Cov}}[\hat{f}, \hat{R}]\}$$

where $\hat{N}_2 = \hat{N}_1 - \hat{R}$ and where $\hat{\text{Cov}}[\hat{f}, \hat{R}]$ depends on the sampling design. The estimator for our situation is given in the Appendix. Equation (13) is more general than the one given by Seber (1982, p. 371) because Seber assumed that $\hat{f}$ and $\hat{R}$ are independent. The estimated variance of $\hat{X}_1$ can be obtained using the delta method:

$$(14)\quad \hat{V}[\hat{X}_1] = (\hat{P}_1 - \hat{P}_2)^{-2}\{\hat{N}_1^2\hat{P}_2^2\hat{V}[\hat{P}_1] + \hat{N}_2^2\hat{P}_1^2\hat{V}[\hat{P}_2] + \hat{P}_1^2\hat{R}^2\hat{V}[\hat{f}] + \hat{P}_1^2(\hat{f} - \hat{P}_2)^2\hat{V}[\hat{R}] + 2\hat{R}\hat{P}_1^2(\hat{f} - \hat{P}_2)\,\hat{\text{Cov}}[\hat{f}, \hat{R}]\}$$

Index-Removal Method

Provided the expected value of the catch rate (catch in number per set) is proportional to the population size, the ratio of expected catch rates before and after the fishery, $E(\hat{c}_1)$ and $E(\hat{c}_2)$, is equal to the ratio of population sizes before and after the fishery, N_1 and N_2 (see Ricker 1975, p. 149; Seber 1982, p. 376), i.e., $E(\hat{c}_1)/E(\hat{c}_2) = N_1/N_2$. Replacing expected values by their estimates, $\hat{c}_1$ and $\hat{c}_2$, yields the expression

$$(15)\quad \hat{N}_1 = \frac{\hat{c}_1(N_1 - N_2)}{\hat{c}_1 - \hat{c}_2}.$$

Assuming that the population is closed between the two times that the population is sampled (except for removals by the fishery), the estimated total catch in number, $\hat{R}$, can be substituted for $N_1 - N_2$ and

$$(16)\quad \hat{N}_1 = \hat{R}\frac{\hat{c}_1}{\hat{c}_1 - \hat{c}_2}.$$

This estimator was first given by Petrides (1949) and was studied by Chapman and Murphy (1965) and Eberhardt (1982). Seber (1982) treated it as a special case of change-in-ratio estimation. Routledge (1989) described a multisample, multiremoval extension.

The method requires the assumption that all animals have the same probability of being captured (by one unit of effort) in the research surveys. Clearly this is not the case if the research survey sampling is selective for x-type crab. However, one can estimate the population of legal-size crab by using an equation analogous to (16):

$$(17)\quad \hat{X}_1 = \hat{R}_x\frac{\hat{c}_{x1}}{\hat{c}_{x1} - \hat{c}_{x2}}$$

where $\hat{c}_{x1}$ and $\hat{c}_{x2}$, the catch rates for x-type crab from surveys before and after the fishery, respectively, can be obtained from equation (3).

If an unbiased estimate is available of the proportion of x-type animals in the population, the population number of snow crab before the fishery, N_1, can be estimated from the results of equation (17) by

$$(18)\quad \hat{N}_1 = \frac{\hat{X}_1}{\hat{P}_1}.$$

The estimated variance of the estimated population size of x-type snow crab, $\hat{V}[\hat{X}_1]$, and the estimated variance of $\hat{N}_1$, $\hat{V}[\hat{N}_1]$, can be obtained by the delta method:

$$(19)\quad \hat{V}[\hat{X}_1] = \frac{\hat{X}_1^2\hat{V}[\hat{c}_{x2}] + \hat{X}_2^2\hat{V}[\hat{c}_{x1}] + \hat{c}_{x1}^2\,\hat{V}[\hat{R}_x]}{(\hat{c}_{x1} - \hat{c}_{x2})^2}$$

$$(20)\quad \hat{V}[\hat{N}_1] = \frac{\hat{V}[\hat{X}_1]}{\hat{P}_1^2} + \frac{\hat{X}_1^2\hat{V}[\hat{P}_1]}{\hat{P}_1^4} + \frac{2\hat{X}_1\hat{R}_x\hat{c}_{x2}}{\hat{P}_1^3(\hat{c}_{x1} - \hat{c}_{x2})^2}\,\hat{\text{Cov}}\,[\hat{P}_1, \hat{c}_{x1}]$$

where the covariance, $\hat{\text{Cov}}\,[\hat{P}_1, \hat{c}_{x1}]$, can be estimated by equation (A7) in the Appendix.

Combined Method

If the change-in-ratio and index-removal estimators provide similar results, it becomes of interest to see if the methods can be combined so that all of the data can be used to provide a better estimate. We develop such a combined estimator below.

Two unbiased estimates can be combined by computing a weighted mean. Let $\hat{X}_{\text{cir}}$ be the change-in-ratio estimator and $\hat{X}_{\text{ir}}$ be the index-removal estimator of the population of legal-size crab before the fishery. The combined estimator, $\hat{X}_{\text{com}}$, is given by

$$(21)\quad \hat{X}_{\text{com}} = \omega\hat{X}_{\text{cir}} + (1 - \omega)\hat{X}_{\text{ir}}$$

where ω is a constant. The variance of the combined estimator is

$$(22)\quad \text{Var}\,[\hat{X}_{\text{com}}] = \omega^2\text{Var}\,[\hat{X}_{\text{cir}}] + (1 - \omega)^2\text{Var}\,[\hat{X}_{\text{ir}}] + 2\omega(1 - \omega)\,\text{Covar}\,[\hat{X}_{\text{cir}}, \hat{X}_{\text{ir}}]$$

and it can be shown that the variance is minimized when ω is chosen to be

$$(23)\quad \omega = \frac{\text{Var}\,[\hat{X}_{\text{ir}}] - \text{Covar}\,[\hat{X}_{\text{cir}}, \hat{X}_{\text{ir}}]}{\text{Var}\,[\hat{X}_{\text{cir}}] + \text{Var}\,[\hat{X}_{\text{ir}}] - 2\,\text{Covar}\,[\hat{X}_{\text{cir}}, \hat{X}_{\text{ir}}]}.$$

Here, Var $[\cdot]$ and Covar $[\cdot]$ refer to the true (not estimated) variance and covariance, respectively. In practice, the combined estimator, $\hat{X}_{\text{com}}$, would be computed using an estimate of ω which is obtained by substituting estimates of the variances and the covariance into equation (23). It remains only to determine an estimator for the covariance of $\hat{X}_{\text{cir}}$ and $\hat{X}_{\text{ir}}$ (see Appendix).

Note that one usually uses a weighted mean to combine two independent estimates. In that case, the weight ω must be in the interval from 0 to 1. In our case, the two estimates of population size are not independent, so the weight ω is not confined to the interval from 0 to 1. We recommend that if the estimate of ω is greater than 1.0, then just the change-in-ratio estimate should be accepted; if the estimate of ω is less than zero, then the index-removal estimate should be used.

The total population of crab greater than or equal to 78 mm CW (N) can be estimated by an analogous procedure. One need only substitute the letter N for each occurrence of the letter X in equations (21), (22), and (23).

Exploitation Rate

The exploitation rate, u, is the fraction of the population removed by the fishery. This can be estimated by

$$(24)\quad \hat{u} = \frac{\hat{R}}{\hat{N}_1}.$$

The exploitation rate for x-type snow crab removed by the fishery is estimated by

$$(25)\quad \hat{u}_x = \frac{\hat{R}_x}{\hat{X}_1}.$$

These can be estimated using results from either the change-in-ratio or index-removal or combined methods. Variance estimators are given in the Appendix.

TABLE 2. Observed proportions ($\hat{P}$) and catch rates of x-type (legal-size) snow crab ($\hat{c}_x$) in the research sampling, for each trap type (large and small mesh), based on 40 sets before the fishery and 41 sets after the fishery in St. Mary's Bay. SE = standard error = $\sqrt{\text{variance}}$.

	Before fishery				After fishery			
Mesh	$\hat{P}$	SE	$\hat{c}_x$	SE	$\hat{P}$	SE	$\hat{c}_x$	SE
Large	0.5425	0.01523	98.35	6.95	0.4893	0.02036	89.39	7.93
Small	0.3407	0.02222	39.95	3.64	0.2703	0.02034	32.39	3.65

Catchability Coefficient and Fishing Power of the Gear

The catchability coefficient, q, is the fraction of the population that is captured by one unit of effort. This can be estimated for the research sampling gear by

$$(26)\qquad \hat{q} = \frac{\hat{c}_1}{\hat{N}_1}$$

or by

$$(27)\qquad \tilde{q} = \frac{\hat{c}_2}{\hat{N}_2} = \frac{\hat{c}_2}{\hat{N}_1 - \hat{R}}\,.$$

Here, $\hat{N}_1$ can be either the change-in-ratio, index-removal, or combined estimator of population size. Equations (26) and (27) give identical results when the index-removal population estimator is used to get $\hat{N}_1$ and $\hat{N}_2$. In general, the two equations will give different estimates when the change-in-ratio or the combined estimator is used.

If the probability of being caught by the research sampling gear is different for x- and y-type animals, the catchability coefficient will change as the population is depleted. In this case, it is appropriate to compute the catchability coefficient for legal-size crab, q_x, by

$$(28)\qquad \hat{q}_x = \frac{\hat{c}_{x1}}{\hat{X}_1}\,.$$

It would be interesting to compare estimates of gear performance among similar stocks. However, estimates of the catchability coefficient are not comparable because they depend on the area inhabited by the stock (Paloheimo and Dickie 1964; Winters and Wheeler 1985). Intuitively, it can be seen that one unit of effort catches a larger proportion of a stock inhabiting a small geographic region than if the same stock inhabits a large region. More formally,

$$(29)\qquad q = \frac{E(h)}{N} = \frac{\rho a \phi}{\phi A} = \frac{\rho a}{A}$$

where the expected catch (or harvest) from one unit of effort, $E(h)$, is the product of the area fished by the gear, a, the proportion of animals encountering the gear that are retained, ρ, and the density of animals, $\phi (E(h) = \rho a \phi)$; the population size, N, is the product of the density of the animals times the area encompassed by the stock, A, $(N = \phi A)$. Thus, q will be inversely related to the area inhabited by the stock (for given gear characteristics ρ and a).

While values of q are not directly comparable among stocks, values of the product qA $(=\rho a)$ are comparable. Furthermore, qA can be interpreted as the fishing power of the gear and thus has an intuitive interpretation. For St. Mary's Bay, we take as the area inhabited by the stock that portion of the Bay deeper than 40 m ($=660.87$ km^2).

Results

Removals of Snow Crab

The quota for snow crab in 1991 was 300 t and the actual catch as determined from the official catch statistics was 317 t. The mean individual weight in the landings, $\bar{W}$, was estimated from plant sampling data to be 460.79 g with a standard error of 6.43. Therefore, the total catch in number, $\hat{R}$, was estimated from equation (7) to be 687 949 with a standard error of 9606. The observed proportion of x-type crab in the catch was $\hat{f} = 0.9134$ with a standard error of 0.01218. The number of x-type crab removed, $\hat{R}_x$, was estimated to be 628 373 with a standard error of 7842.

Estimates of the Proportions and Catch Rates

The estimates of the proportions of x-type crab before and after the fishing season, $\hat{P}_1$ and $\hat{P}_2$, and the estimated variances, $\hat{V}[\hat{P}_1]$ and $\hat{V}[\hat{P}_2]$, were obtained using equations (1) and (2). Catch rates and the variances were estimated using equations (3) and (4) (Table 2).

Estimates of Population Size, Exploitation Rate, and Catchability

Estimates of population size were obtained for two trap types using the change-in-ratio estimator, the index-removal estimator, and the combined method (Table 3). The weighting factor, ω, for the combined method for the total population ($\geqslant$78 mm CW) was estimated to be 0.9803 and 1.0971, respectively, for large- and small-mesh traps. For the legal-size (x-type) crab population, it was estimated to be 0.9792 and 1.0725, respectively, for large- and small-mesh traps. When the value of ω was less than 1, we did not comute the combined estimators. The exploitation rate was then estimated using equations (24) and (25) from the results shown in Table 3 (Table 4).

Because each set had four large-mesh traps and two small-mesh traps, the catch rates should be standardized before comparing the catchabilities, i.e., the catch rates should be divided by 4 for large-mesh traps and by 2 for small-mesh traps. The catchability coefficient for legal-size crab is estimated using equation (28) from the results of the change-in-ratio, index-removal, and combined methods and then changed into fishing power (qA) by multiplying by the area (660.87 km^2) (Table 5).

Discussion

Evaluation of Results

The estimates of the size of the exploited population were rather variable (Table 3: range of estimates of X_1 from 2141×10^3 to 6897×10^3, range of CVs from 31.61 to 113.14). This can be attributed to three possible factors: amount of sampling effort, level of exploitation, and biases due to failure of assumptions.

TABLE 3. Estimates of population size of snow crab in St. Mary's Bay by trap type before and after the fishery in 1991 using change-in-ratio (CIR), index-removal (IR), and combined (COM) estimators ($\times 10^3$). SE = standard error. For reasons discussed in the text, the estimates of legal-size crab ($\hat{X}_1$ and $\hat{X}_2$) are believed to be more reliable than those of the total population ≥78 mm CW ($\hat{N}_1$ and $\hat{N}_2$).

	Large-mesh trap			Small-mesh trap	
Parameter	CIR	IR	COM	CIR	IR
$\hat{N}_1$	5484	12 714	5627	6284	9746
$\hat{X}_1$	2975	6897	3057	2141	3321
$\hat{N}_2$	4796	12 026	4976	5596	9058
$\hat{X}_2$	2347	6269	2446	1513	2692
SE [$\hat{N}_1$]	2419	14 410	2402	2561	6089
SE [$\hat{X}_1$]	1260	7804	1249	770	2062

TABLE 4. Estimates of the exploitation rate of snow crab, $\hat{u}$, and the exploitation rate of legal-size snow crab, $\hat{u}_x$, in St. Mary's Bay by trap type using the population number from change-in-ratio (CIR), index-removal (IR), and combined (COM) methods. For reasons described in the text, the estimates of u_x are believed to be more reliable than those of u.

	Large-mesh trap			Small-mesh trap	
Parameter	CIR	IR	COM	CIR	IR
$\hat{u}$	0.1254	0.05411	0.1223	0.1095	0.07059
$\hat{u}_x$	0.2112	0.09110	0.2056	0.2935	0.1892
SE [$\hat{u}$]	0.05537	0.06133	0.07101	0.04463	0.04410
SE [$\hat{u}_x$]	0.08934	0.1031	0.08392	0.1054	0.1175

We had planned to make 80 sets during each of two cruises. However, because of logistical problems during both cruises, only half the number of sets could be made (40, first cruise; 41, second cruise). Doubling the number of sets reduces the variances and covariances of the inputs by half. We recomputed the coefficients of variation of the estimates of the exploited population ($\hat{X}_1$) with estimated variances and covariances of the inputs cut by 50% in order to see what precision we might have had if we could have sampled as originally planned. The resulting CVs ranged from 22.4 to 80.0.

The change-in-ratio and index-removal methods work best when the exploitation rate is high so that the catch rate and population composition are greatly affected by the removal. This is reflected in the variance estimator for the change-in-ratio method (equation (13)) where the expression $(\hat{P}_1 - \hat{P}_2)^2$ appears in the denominator. Similarly, the variance estimator for the index-removal method (equation (19)) has the expression $(\hat{c}_{x1} - \hat{c}_{x2})^2$ in the denominator. In our example, the proportions and the catch rates did not change much from the first survey to the second, thus contributing to high variance. Despite the somewhat high variability in population estimates, results from both methods indicate that the exploitation rate is light to moderate (Table 4: lowest estimate of u_x = 9.11%, highest estimate = 29.35%).

The third possible reason for variability among the estimates of population size is differential sensitivity of the methods to failures of the assumptions. The assumptions inherent in the use of the change-in-ratio estimator, and the consequences of violating the assumptions, are well known (see Seber 1982, chap. 9). The index-removal method has received much less attention (see Seber 1982, chap. 9) and little work has been done to compare the methods (Roseberry and Woolf 1991).

The principal assumptions behind the change-in-ratio and index-removal methods are similar (Table 6). However, the assumptions for the index-removal method are stronger than those for the change-in-ratio method. Of particular note is the problem of catchability in the research surveys varying according to the size of the animal or other factors. For the index-removal method, this problem of heterogeneity can be minimized by computing index-removal estimates separately for each exploited size class. For the change-in-ratio method, the estimates of total abundance are biased in general when the catchability of the two groups varies in the research surveys. However, there is an important exception: when removals are made from only one group, then the estimate for that group is unbiased. Thus, the change-in-ratio estimator should give nearly ubiased estimates of the legal-size crab population, since 91% of the removals are estimated to be of legal size. The estimates of the immediate prerecruits are probably too low because the catchability of prerecruits is probably less than that of legal-size crab. Therefore, it might be appropriate to estimate the exploitation rate and catchability coefficient of x-type animals instead of the two groups combined.

TABLE 5. Estimates of the fishing power of the gear, $\hat{q}A$, for legal-size crab. Estimates were obtained from the results of the change-in-ratio (CIR), index-removal (IR), and combined (COM) methods for each trap type (large and small mesh). The area inhabited by the stock, A, is taken to be 660.87 km^2.

Mesh	CIR	IR	COM
Large	0.005462	0.002356	0.005316
Small	0.006166	0.003975	—

Estimates of the fishing power (qA) of large-mesh traps (same type as used in the commercial fishery) for legal-size crab ranged from 0.0024 to 0.0055 (Table 5). Hoenig et al. (1992) estimated the fishing power of the large-mesh traps from 60 Leslie analyses of commercial catch-rate data from nine stocks. Their estimate of qA = 0.005 is within the range of estimates reported here.

TABLE 6. Comparison of principal assumptions behind the change-in-ratio (CIR) and index-removal (IR) methods.

Assumption	Method	Description
1	CIR	Population is closed or, alternatively, mortality rate and immigration/emigration rates are the same for both groups
1	IR	Population is closed or, alternatively, additions equal losses (excluding the removal)
2	CIR	All animals have the same probability of being caught in the jth research survey ($j = 1, 2$) or, alternatively, if x-type and y-type animals have different probabilities but removal of y-type animals $= 0$, then $\hat{X}$ is asymptotically unbiased but $\hat{N}$ is biased
2	IR	All animals have the same probability of being caught by one unit of sampling effort in the research surveys, i.e., probability of capture does not vary within or between surveys

Methodological Issues

We presented the change-in-ratio and index-removal methods as moment-type estimators. Seber (1982) pointed out that the change-in-ratio estimator (11) is the maximum likelihood estimator for three models: (1) $\hat{P}_j$ is a binomially distributed random variable, (2) $\hat{P}_j$ is distributed hypergeometrically, and (3) the catches of x- and y-type individuals are independent Poisson random variables. Eberhardt (1982) pointed out that the index-removal estimator (equation (15)) is the maximum likelihood estimator when the pre- and postseason survey catches are Poisson random variables. In fact, these results can be generalised considerably. Whenever the estimators of the inputs to these models are maximum likelihood, the resulting estimates of population size are maximum likelihood. This follows immediately by the invariance principle of maximum likelihood estimation (see Freund 1971). It is reassuring that the moment estimator is the maximum likelihood estimator for a wide variety of sampling distributions. Note, however, that the variance of the population estimator does depend on the underlying sampling distributions. Fortunately, there is another general result that can be invoked to simplify things. The variance formula obtained by the delta method gives the same results as the one derived from the likelihood function (by inverting the information matrix) when two conditions are met: the data are from the exponential family of distributions (e.g., Poisson, binomial, hypergeometric, normal) and the dimensionality of the minimally sufficient statistic is equal to the number of parameters (Brownie et al. 1985, p. 213–215). This means that the variance formulae in this paper are appropriate for maximum likelihood estimation under a variety of underlying models.

Confidence intervals can be constructed in the usual way, e.g., the estimate plus and minus 2 standard errors for a 95% confidence interval. Here, the standard errors were obtained by the delta method. Although this procedure is asymptotically valid, it may not perform well when sample sizes are not large because of a lack of normality. An alternative is to construct interval estimates based on likelihood ratios (e.g., Routledge 1989; Cormack 1992).

Chapman (1955) studied the optimal way to allocate sampling effort to the pre- and postseason surveys when using the change-in-ratio method. For a wide range of conditions (including those found in St. Mary's Bay), the optimal design is to allocate roughly 50% of the sampling effort to each survey. Optimal design has not been studied for the index-removal method.

Usefulness of the Methods

It is curious that these methods have rarely been used in fisheries research and assessment even though they are well known to wildlife scientists (e.g., Roseberry and Woolf 1991). One reason may be the high cost: it is necessary to sample the population both before and after the fishery. Another plausible explanation is simply the lack of awareness of these methods among fishery scientists.

The kinds of data required — catch rates and catch composition — are commonly collected in research surveys. The assumptions required for valid use of the methods are modest (Seber 1982), especially when compared with alternative models such as Petersen mark–recapture estimates or Leslie analyses of commercial catch and effort data. In general, it is a good idea to estimate key population parameters by more than one method when possible. It is reassuring when the conclusions drawn about a population do not depend critically on the model chosen for the assessment. Alternatively, if the results from different methods differ substantially, then this is an indication that further study is required to determine which, if any, method provides reasonable results. The use of the change-in-ratio and index-removal methods provides an opportunity to assess the reliability of the results. In addition, these methods can be combined with mark–recapture methods and, possibly, with catch-effort models such as a Leslie or DeLury estimator. For example, Chapman (1955) showed how to combine the change-in-ratio and Petersen mark–recapture methods.

In the present case, results from the change-in-ratio method affected the combined estimate more greatly than did results from the index-removal method because ω (ranging from 0.8725 to 0.9751) was close to 1. Hence the estimates from the combined and the change-in-ratio method were similar.

In addition to providing estimates of pre- and postseason abundance, the methods can provide estimates of exploitation rate, catchability coefficient, and possibly prerecruit abundance. The precision and accuracy attainable in practice remain to be determined. However, knowledge about the catchability coefficient in research surveys can be expected to improve as the methods are applied repeatedly. If the catchability coefficient is known sufficiently well, the preseason abundance can be determined from a single survey by dividing the catch rate by the estimated catchability coefficient (Seber and Le Cren 1967, p. 636; Seber 1982, p. 324–325):

$$\hat{X} = \frac{\hat{c}_x}{\hat{q}_x} .$$

The estimated variance is obtained by the delta method as

$$\hat{V}[\hat{X}] = \frac{1}{\hat{q}_x^{\,2}} \hat{V}[\hat{c}_x] + \frac{\hat{c}_x^{\,2}}{\hat{q}_x^{\,4}} \hat{V}[\hat{q}_x] .$$

The use of research surveys before and after the fishery, combined with commercial catch sampling, provides the scientist with the opportunity to estimate a number of key parameters by several methods. It also enables the scientist to refine the estimate of the catchability coefficient if the approach is applied repeatedly. These considerations lead us to believe that the change-in-ratio and index-removal methods should receive more attention from fishery scientists studying closed populations.

Acknowledgements

We thank Joe Drew, Paul Beck, and Gerry Dawe for assistance in the field and Kenneth Pollock, William Warren, Russell Millar, John Wheeler, and the anonymous reviewers for helpful discussions.

References

Brownie, C., K.P. Burnham, D.R. Anderson, and D.S. Robson. 1985. Statistical inference from band recovery data — a handbook 2nd ed. Resour. Publ. U.S. Dep. Inter. Fish Wild. Serv. 156: 305 p.

Chapman, D.G. 1955. Population estimation based on change of composition caused by selective removal. Biometrika 42: 279–290.

Chapman, D.G. 1964. A critical study of Pribilof fur seal population estimates. Fish. Bull. 63: 657–669.

Chapman, D.G., and G.I. Murphy. 1965. Estimates of mortality and population from survey-removal records. Biometrics 21: 921–935.

Cochran, W.G. 1977. Sampling techniques. 3rd. ed. John Wiley & Sons, New York, N.Y. 428 p.

Cormack, R.M. 1992. Interval estimation for mark–recapture studies of closed populations. Biometrics 48: 567–576.

Davis, D.E. 1963. Estimating the numbers of game populations, p. 89–118. *In* H.S. Mosby [ed.] Wildlife investigational techniques. 2nd ed. The Wildlife Society, Washington, D.C.

Dawe, E.G., J.M. Hoenig, P.G. O'Keefe, and M. Moriyasu. 1992. Molt indicators and growth increments for male snow crabs (*Chionoecetes opilio*) from Newfoundland. Int. Counc. Explor. Sea C.M. 1992/K35: 15 p.

Eberhardt, L.L. 1982. Calibrating an index by using removal data. J. Wildl. Manage. 46: 734–740.

Freund, J.E. 1971. Mathematical statistics. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J. 463 p.

Hoenig, J.M., E.G. Dawe, D.M. Taylor, M. Eagles, and J. Tremblay. 1992. Leslie analyses of commercial trap data: a comparative study of the catchability coefficient for male snow crab (*Chionoecetes opilio*). Int. Counc. Explor. Sea C.M. 1992/K:34: 8 p.

Kelker, G.H. 1940. Estimating deer populations by a differential hunting loss in the sexes. Proc. Utah Acad. Sci. Arts. Lett. 17: 6–69.

Lander, R.H. 1962. A method of estimating mortality rates from change in composition. J. Fish. Res. Board. Can. 19: 159–168.

Miller, R.J., and P.G. O'Keefe. 1981. Seasonal and depth distributions, size, and molt cycle of the spider crabs, *Chionoecetes opilio, Hyas araneus,* and *Hyas coarctatus*, in a Newfoundland Bay. Can. Tech. Rep. Fish. Aquat. Sci. 1003: iv + 18 p.

Murphy, G.I. 1952. An analysis of silver salmon counts at Benkow Dam, South Fork of Eel River, California. Calif. Fish Game 38: 105–112.

Paloheimo, J.E., and L.M. Dickie. 1964. Abundance and fishing success. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 155: 152–163.

Paulik, G.J., and D.S. Robson. 1969. Statistical calculations for change-in-ratio estimators of population parameters. J. Wildl. Manage. 33: 1–27.

Petrides, G.A. 1949. View points on the analysis of open season sex and age ratios. Trans. N. A. Wildl. Conf. 14: 391–410.

Pollock, K.H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present and future. J. Am. Stat. Assoc. 86: 225–238.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

Roseberry, J.L., and A. Woolf. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildl. Monogr. 117: 1–59.

Routledge, R.D. 1989. The removal method for estimating natural populations: incorporating auxiliary information. Biometrics 45: 111–121.

Rupp, R.S. 1966. Generalized equation for the ratio method of estimating population abundance. J. Wildl. Manage. 30: 523–526.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Macmillan, New York, N.Y. 654 p.

Seber, G.A.F., and E.D. Le Cren. 1967. Estimating population parameters from catches large relative to the population. J. Anim. Ecol. 36: 631–643.

Taylor, D.M. 1992. Long-term observations on movements of tagged male snow crabs in Bonavista Bay, Newfoundland. N. A. J. Fish. Manage. 12: 777–782.

Taylor, D.M., and W.G. Warren. 1991. Male snow crab, Chionoecetes opilio (Fabricius, 1788), weight–width relationships: an exercise in multisource regression. J. Shellfish Res. 10: 165–168.

Winters, G.H., and J.P. Wheeler. 1985. Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. 42: 989–998.

Appendix. Descriptions of Some Variance Estimators

Variance of Mean Individual Weight and Number Removed

A simple plan for sampling the landings is one-stage cluster sampling. This would entail making a list of all crab plant × day combinations (clusters), randomly selecting M clusters to sample, and obtaining the mean weight of all crab landed in each sampled cluster. For this design, the estimated mean weight is given by equation (8) and the variance of the mean weight would be estimated by

$$\text{(A1)} \qquad \hat{V}[\bar{W}] = \frac{\sum_{m=1}^{M} (z_m^* \bar{W}_m - z_m^* \bar{W})^2}{M(M-1)\,\bar{z}^{*2}}$$

where $\bar{W}_m$ is the mean individual weight in the mth cluster sample and the other symbols are as in the text.

Often, the number of crab landed in a cluster may be too large to count. In this case, further subsampling (i.e., two-stage cluster sampling) may be convenient. Cochran (1977) contains further details.

In our study, the weights of the crab were estimated from the carapace width rather than measured directly. This adds additional variability to the estimate of mean weight (beyond the sampling error described by equation (A1)). Additionally, because of logistical problems, our sample was not a random sample of the clusters. We use equation (A1) as an approximate estimate of the variance but recognize that this probably underestimates the variance.

If it had been necessary to obtain an estimate, $\hat{L}$, of the total catch in weight, L, the estimated variance of $\hat{R}$ (equation (7)) would be obtained using the delta method:

$$\hat{V}[\hat{R}] = \frac{\hat{L}^2}{\bar{W}^4}\hat{V}[\bar{W}] + \frac{1}{\bar{W}^2}\hat{V}[\hat{L}] - \frac{2\hat{L}}{\bar{W}^3}\hat{\text{Cov}}[\hat{L}, \bar{W}] \, .$$

The appropriate estimators for the two variances and the covariance depend on the particular sampling design adopted.

Variance Estimator for $\hat{R}_x$ and Covariance Estimator for $\hat{f}$ and $\hat{R}$

The variance estimator for $\hat{R}_x$ (equation (10)) was obtained by the delta method:

$$\text{(A2)} \quad \hat{V}[\hat{R}_x] = \hat{R}^2\,\hat{V}[\hat{f}] + \hat{f}^2\,\hat{V}[\hat{R}] + 2\hat{f}\,\hat{R}\,\hat{\text{Cov}}[\hat{f}, \hat{R}]\ .$$

The estimated covariance of $\hat{f}$ and $\hat{R}$ is obtained using the delta method:

$$\text{(A3)} \quad \hat{\text{Cov}}[\hat{f}, \hat{R}] = -\frac{L\bar{x}^*}{\bar{z}^{*2}\,\bar{W}^*}\hat{V}[\bar{z}^*] + \frac{L\bar{x}^*}{\bar{z}^*\,\bar{W}^{*2}}\hat{\text{Cov}}[\bar{z}^*, \bar{W}^*] + \frac{L}{\bar{z}^*\,\bar{W}^*}\hat{\text{Cov}}[\bar{x}^*, \bar{z}^*] - \frac{L}{\bar{W}^{*2}}\hat{\text{Cov}}[\bar{x}^*, \bar{W}^*]$$

where $\bar{x}^*$ is the mean number of x-type animals per plant sample, $\bar{z}^*$ is the mean size of the plant samples,

$$\bar{W}^* = \frac{\sum_{m=1}^{M} W_m^*}{M}\ ,$$

and W_m^* is the total weight in the mth plant sample.

The variance of $\bar{z}^*$ can be estimated in the usual way by

$$\hat{V}[\bar{z}^*] = \frac{\sum_{m=1}^{M}(z_m^* - \bar{z}^*)^2}{M(M-1)}\ .$$

The covariances, $\hat{\text{Cov}}[\bar{z}^*, \bar{W}^*]$, $\hat{\text{Cov}}[\bar{x}^*, \bar{z}^*]$, and $\hat{\text{Cov}}[\bar{x}^*, \bar{W}^*]$, can be estimated from the samples by

$$\hat{\text{Cov}}[\bar{z}^*, \bar{W}^*] = \frac{\sum_{m=1}^{M}(z_m^* - \bar{z}^*)(W_m^* - \bar{W}^*)}{M(M-1)}$$

$$\hat{\text{Cov}}[\bar{x}^*, \bar{z}^*] = \frac{\sum_{m=1}^{M}(x_m^* - \bar{x}^*)(z_m^* - \bar{z}^*)}{M(M-1)}$$

$$\hat{\text{Cov}}[\bar{x}^*, \bar{W}^*] = \frac{\sum_{m=1}^{M}(x_m^* - \bar{x}^*)(W_m^* - \bar{W}^*)}{M(M-1)}\ .$$

Estimates of $\hat{\text{Cov}}\,[\hat{N}_{\text{cir}}, \hat{N}_{\text{ir}}]$ and $\hat{\text{Cov}}\,[\hat{X}_{\text{cir}}, \hat{X}_{\text{ir}}]$

By the delta method, the estimated covariance of the estimates given by equations (11) and (16) is

$$\text{(A4)} \quad \hat{\text{Cov}}[\hat{N}_{\text{cir}}, \hat{N}_{\text{ir}}] = \frac{\hat{X}_{\text{ir}}}{\hat{R}_x(\hat{P}_1 - \hat{P}_2)\hat{P}_1}\hat{V}[\hat{R}_x] - \frac{\hat{X}_{\text{ir}}\hat{P}_2}{\hat{R}_x(\hat{P}_1 - \hat{P}_2)\hat{P}_1}\hat{\text{Cov}}[\hat{R}, \hat{R}_x] + \frac{(\hat{R}_x - \hat{P}_2\hat{R})\hat{R}_x\hat{c}_{x2}}{(\hat{P}_1 - \hat{P}_2)^2(\hat{c}_{x1} - \hat{c}_{x2})^2\hat{P}_1}\hat{\text{Cov}}[\hat{P}_1, \hat{c}_{x1}]$$
$$+ \frac{\hat{N}_{\text{cir}}\hat{X}_{\text{ir}}}{(\hat{P}_1 - \hat{P}_2)\hat{P}_1^2}\hat{V}[\hat{P}_1] + \frac{(\hat{R}_x - \hat{R}\hat{P}_1)\hat{X}_{\text{ir}}}{(\hat{P}_1 - \hat{P}_2)^2(\hat{c}_{x1} - \hat{c}_{x2})\hat{P}_1}\hat{\text{Cov}}[\hat{P}_2, \hat{c}_{x2}]\ .$$

Similarly, the estimated covariance of the estimates given by equations (12) and (17) is

$$\text{(A5)} \quad \hat{\text{Cov}}[\hat{X}_{\text{cir}}, \hat{X}_{\text{ir}}] = \frac{\hat{P}_2\hat{X}_{\text{cir}}\hat{c}_{x2}\hat{R}_x}{\hat{P}_1(\hat{P}_1 - \hat{P}_2)(\hat{c}_{x1} - \hat{c}_{x2})^2}\hat{\text{Cov}}[\hat{P}_1, \hat{c}_{x1}] + \frac{\hat{P}_1\hat{X}_{\text{ir}}(\hat{R}_x - \hat{P}_1\hat{R})}{(\hat{P}_1 - \hat{P}_2)^2(\hat{c}_{x1} - \hat{c}_{x2})}\hat{\text{Cov}}[\hat{P}_2, \hat{c}_{x2}]$$
$$- \frac{\hat{P}_1\hat{P}_2\hat{X}_{\text{ir}}}{\hat{R}_x(\hat{P}_1 - \hat{P}_2)}\hat{\text{Cov}}[\hat{R}, \hat{R}_x] + \frac{\hat{P}_1\hat{X}_{\text{ir}}}{\hat{R}_x(\hat{P}_1 - \hat{P}_2)}\hat{V}[\hat{R}_x]\ .$$

In the above, $\hat{V}[\hat{R}_x]$ is obtained from equation (A2) while

$$\text{(A6)} \quad \hat{\text{Cov}}[\hat{R}, \hat{R}_x] = \hat{\text{Cov}}[\hat{R}, \hat{f}\hat{R}] = \hat{f}\,\hat{V}[\hat{R}] + \hat{R}\,\hat{\text{Cov}}[\hat{f}, \hat{R}]$$

where $\hat{\text{Cov}}\,[\hat{f}, \hat{R}]$ is from equation (A3) and

$$\text{(A7)} \quad \hat{\text{Cov}}[\hat{P}_j, \hat{c}_{xj}] = \frac{\sum_{i=1}^{n_j} (x_{ij} - \hat{P}_j z_{ij})(x_{ij} - \hat{c}_{xj})}{n_j(n_j - 1)\bar{z}_j}.$$

Variance Estimators for Exploitation Rates, $\hat{u}$ and $\hat{u}_x$

If the results from the change-in-ratio method are used for estimating the exploitation rate, the variance of $\hat{u}$ (equation (24)) can be estimated by (see Seber 1982, p. 380)

$$\text{(A8)} \quad \hat{V}[\hat{u}] = \frac{(\hat{f} - \hat{P}_2)^2\hat{V}[\hat{P}_1] + (\hat{f} - \hat{P}_1)^2\hat{V}[\hat{P}_2] + (\hat{P}_1 - \hat{P}_2)^2\hat{V}[\hat{f}]}{(\hat{f} - \hat{P}_2)^4}$$

and the estimated variance of $\hat{u}_x$ (equation (25)) can be obtained from the delta method:

$$\text{(A9)} \quad \hat{V}[\hat{u}_x] = \frac{\hat{f}^2(\hat{f} - \hat{P}_2)^2\hat{P}_2^2\hat{V}[\hat{P}_1] + \hat{P}_1^2\hat{f}^2(\hat{f} - \hat{P}_1)^2\hat{V}[\hat{P}_2] + \hat{P}_1^2(\hat{P}_1 - \hat{P}_2)^2\hat{P}_2^2\hat{V}[\hat{f}]}{\hat{P}_1^4(\hat{f} - \hat{P}_2)^4}.$$

If the exploitation rate is estimated from the results of the index-removal method, the estimated variances of $\hat{u}$ and $\hat{u}_x$ can be obtained from the delta method:

$$\text{(A10)} \quad \hat{V}[\hat{u}] = \frac{(\hat{c}_{x1} - \hat{c}_{x2})^2}{\hat{f}^2\hat{c}_{x1}^2}\hat{V}[\hat{P}_1] + \frac{\hat{P}_1^2(\hat{c}_{x1} - \hat{c}_{x2})^2}{\hat{f}^4\hat{c}_{x1}^2}\hat{V}[\hat{f}] + \frac{\hat{P}_1^2}{\hat{f}^2\hat{c}_{x1}^2}\hat{V}[\hat{c}_{x2}] + \frac{\hat{P}_1^2\hat{c}_{x2}^2}{\hat{f}^2\hat{c}_{x1}^4}\hat{V}[\hat{c}_{x1}] + \frac{2\hat{P}_1\hat{c}_{x2}(\hat{c}_{x1} - \hat{c}_{x2})}{\hat{f}^2\hat{c}_{x1}^3}\hat{\text{Cov}}[\hat{P}_1, \hat{c}_{x1}]$$

$$\text{(A11)} \quad \hat{V}[u_x] = \frac{\hat{c}_{x2}^2}{\hat{c}_{x1}^4}\hat{V}[\hat{c}_{x1}] + \frac{1}{\hat{c}_{x1}^2}\hat{V}[\hat{c}_{x2}].$$

If the exploitation rate is estimated from the results of the combined method, the estimated variances of $\hat{u}$ and $\hat{u}_x$ can be obtained from the delta method:

$$\text{(A12)} \quad \hat{V}[\hat{u}] = \frac{\hat{R}^2(\hat{P}_1\hat{N}_{\text{com}} - \hat{P}_2(1-\omega)\hat{N}_{\text{ir}})^2}{\hat{P}_1^2(\hat{P}_1 - \hat{P}_2)^2\hat{N}_{\text{com}}^4}\hat{V}[\hat{P}_1] + \frac{\omega^2\hat{R}^2(\hat{N}_{\text{cir}} - \hat{R})^2}{\hat{N}_{\text{com}}^4(\hat{P}_1 - \hat{P}_2)^2}\hat{V}[\hat{P}_2] + \frac{\hat{R}^2(\hat{R}_x\omega + (1-\omega)(\hat{P}_1 - \hat{P}_2)\hat{N}_{\text{ir}})^2}{\hat{f}^2(\hat{P}_1 - \hat{P}_2)^2\hat{N}_{\text{com}}^4}\hat{V}[\hat{f}]$$
$$+ \frac{\hat{R}^2(1-\omega)^2\hat{N}_{\text{ir}}^2\hat{c}_{x2}^2}{\hat{c}_{x1}^2(\hat{c}_{x1} - \hat{c}_{x2})^2\hat{N}_{\text{com}}^4}\hat{V}[\hat{c}_{x1}] + \frac{\hat{R}^2(1-\omega)^2\hat{N}_{\text{ir}}^2}{\hat{N}_{\text{com}}^4(\hat{c}_{x1} - \hat{c}_{x2})^2}\hat{V}[\hat{c}_{x2}] + \frac{2\hat{N}_{\text{ir}}^2\hat{R}_x\hat{c}_{x2}(1-\omega)(\hat{P}_1\hat{N}_{\text{com}} - \hat{P}_2(1-\omega)\hat{N}_{\text{ir}})}{\hat{f}^2\hat{N}_{\text{com}}^4\hat{c}_{x1}(\hat{P}_1 - \hat{P}_2)}\hat{\text{Cov}}[\hat{P}_1, \hat{c}_{x1}]$$
$$+ \frac{2\hat{R}^2\omega(1-\omega)\hat{N}_{\text{ir}}(\hat{N}_{\text{cir}} - \hat{R})}{\hat{N}_{\text{com}}^4(\hat{P}_1 - \hat{P}_2)(\hat{c}_{x1} - \hat{c}_{x2})}\hat{\text{Cov}}[\hat{P}_2, \hat{c}_{x2}]$$

$$\text{(A13)} \quad \hat{V}[\hat{u}_x] = \frac{\hat{R}_x^2\omega^2\hat{P}_2^2\hat{N}_{\text{cir}}^2}{\hat{X}_{\text{com}}^4(\hat{P}_1 - \hat{P}_2)^2}\hat{V}[\hat{P}_1] + \frac{\hat{R}_x^2\omega^2(\hat{P}_1\hat{R} - \hat{X}_{\text{cir}})^2}{\hat{X}_{\text{com}}^4(\hat{P}_1 - \hat{P}_2)^2}\hat{V}[\hat{P}_2] + \frac{\hat{R}^4\omega^2\hat{P}_1^2\hat{P}_2^2}{\hat{X}_{\text{com}}^4(\hat{P}_1 - \hat{P}_2)^2}\hat{V}[\hat{f}]$$
$$+ \frac{\hat{R}_x^4(1-\omega)^2\hat{c}_{x2}^2}{\hat{X}_{\text{com}}^4(\hat{c}_{x1} - \hat{c}_{x2})^4}\hat{V}[\hat{c}_{x1}] + \frac{(1-\omega)^2\hat{X}_{\text{ir}}^4}{\hat{X}_{\text{com}}^4\hat{c}_{x1}^2}\hat{V}[\hat{c}_{x2}] + \frac{2\hat{R}_x^3\omega(1-\omega)\hat{c}_{x2}\hat{P}_2\hat{N}_{\text{cir}}}{\hat{X}_{\text{com}}^4(\hat{P}_1 - \hat{P}_2)(\hat{c}_{x1} - \hat{c}_{x2})^2}\hat{\text{Cov}}[\hat{P}_1, \hat{c}_{x1}]$$
$$+ \frac{2\hat{R}_x\omega(1-\omega)\hat{X}_{\text{ir}}^2(\hat{X}_{\text{cir}} - \hat{P}_1\hat{R})}{\hat{X}_{\text{com}}^4\hat{c}_{x1}(\hat{P}_1 - \hat{P}_2)}\hat{\text{Cov}}[\hat{P}_2, \hat{c}_{x2}].$$

Here, we treat the weighting factor ($\hat{\omega}$) as a constant (ω) rather than as a random variable.