

**Abstract.**—The catch equation used in virtual population analysis (VPA), and most annual age-structured methods, assumes a constant fishing mortality rate ( $F$ ) throughout the year even though many, if not most, fisheries are seasonal. Breaking this assumption of a constant  $F$  creates a bias in the resulting population-size estimates when the observed catch is used as input in VPA. The bias can be reduced by changing the time step in the analysis to quarters or months, as has been suggested in the past, but this change is not always easy or practical. This paper presents an alternative method for reducing the bias: correction of the catch values to meet the assumption of a constant fishing mortality rate. A simple algorithm is presented that gives the number of fish that would have been caught from a given population if the observed fishing mortality rate had been spread evenly throughout the year. An iterative process improves the required guess for the population size such that the bias is eliminated.

## Correcting annual catches from seasonal fisheries for use in virtual population analysis

Christopher M. Legault  
Nelson M. Ehrhardt

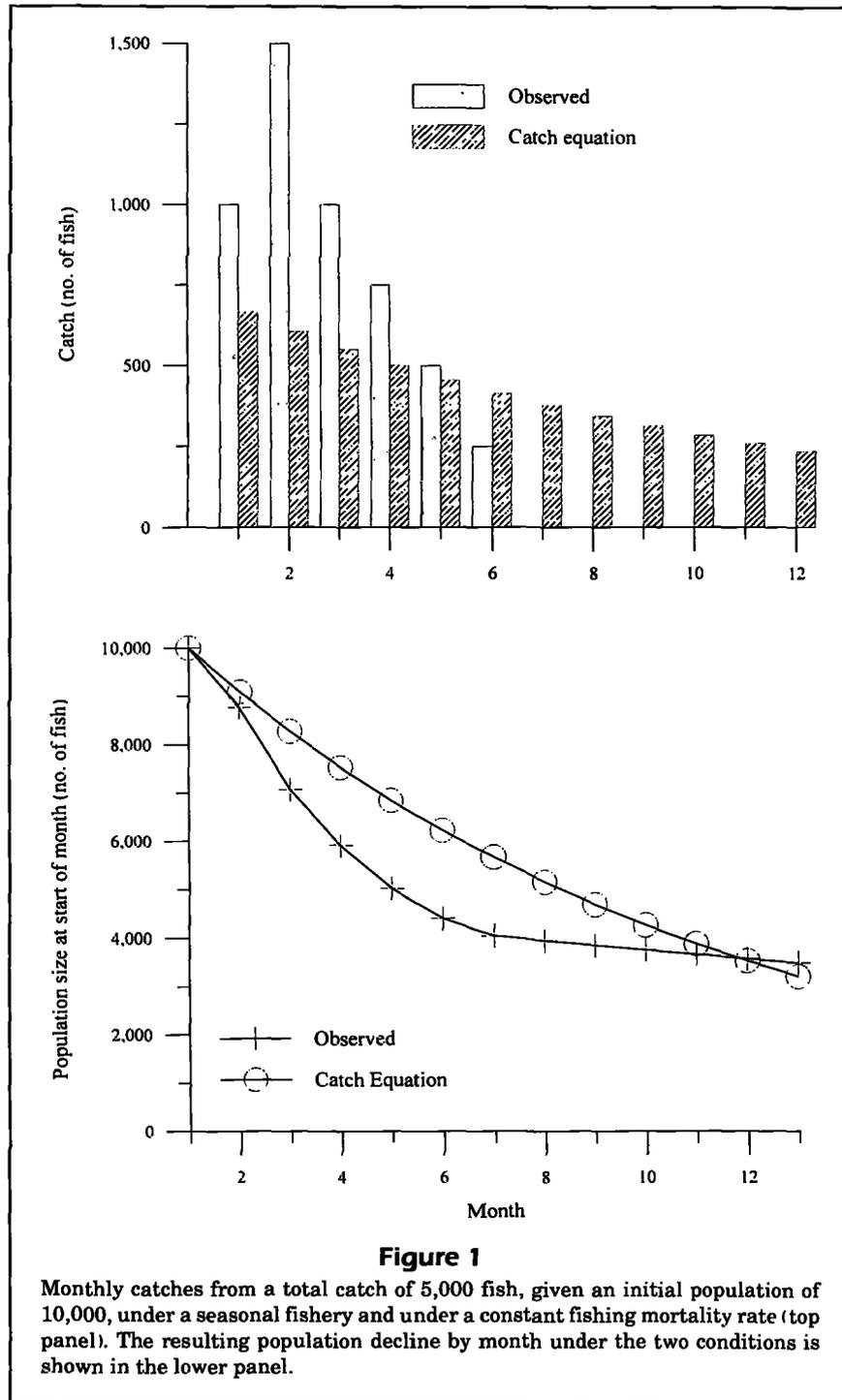
Division of Marine Biology and Fisheries  
Rosenstiel School of Marine and Atmospheric Science  
University of Miami  
4600 Rickenbacker Causeway, Miami, Florida 33149  
E-mail address: clegault@rsmas.miami.edu

Many, if not most, fisheries operate during only part of the year. The seasonal nature of fisheries is caused by quota and regulatory limitations, weather conditions, and fish availability among other reasons. The catch equation used in virtual population analysis (VPA) and in other annual age-structured analyses, assumes that a constant fishing mortality rate is applied continuously throughout the year. Under this assumption, a bias will be introduced into the analysis when the fishery is in fact seasonal. With the catch equation, the total catch is assumed to be distributed throughout the year, such that it follows the exponential decline of the population. The resulting total mortality rate inferred from the decline of the population with the catch equation is different from what actually occurred in the population. For example, given a total catch of 5,000 fish distributed unevenly during the first half of the year (Fig. 1, top panel), the population numbers at the end of the year would be negatively biased with the assumption inherent in the catch equation (Fig. 1, lower panel).

This bias has been examined in the past and found to be at a low level for most situations; exceptions occur for heavily exploited fisheries that occur during either the first or last quarter of the year. The fact that seasonal catches cause the es-

timated exploitation rate to be biased was described by Youngs (1976). The impact of seasonal catches on population-size estimates from cohort analysis was explored by Ulltang (1977), who recommended using smaller time units than a year to overcome the errors. Sims (1982) used both analytic methods and simulation to demonstrate the effects of seasonal catches on cohort analysis, concluding that the relative errors in population-size estimates are not severe unless the natural mortality rate is large or the fishery is heavily exploited, or both. The traditional recommendation for seasonal fisheries is to change the time scale from year to quarter or month so that the fishing mortality rate will be approximately constant within the time unit. The conversion from annual to monthly or to some other time step is not always simple, either in the coding of programs or in the collection of data. For example, the creation of adequate age-length keys for ageing the catch under monthly or even quarterly time steps could require prohibitively expensive sampling schemes and would be technically challenging.

A more recent approach to deal with the problem of seasonal fisheries is the generalization of the equations used in virtual population analysis. An attempt to remove the



bias caused by seasonal fisheries was made by MacCall (1986) who provided a family of approximations to virtual population analysis based on Pope's (1972) cohort analysis. Hiramatsu (1995) generalized the equations to allow for a constant catch rate within a season, and Mertz and Myers (1996) reformulated the equations to allow for any seasonal pattern of catches. Most current software available for virtual

population analysis and other age-structured analyses are designed for constant fishing mortality rates and annual time steps, however. Reformulating the basic equations used in virtual population analysis may not be practical for situations where a given algorithm is used that is already quite complex. An alternative to changing the time scale or modifying the equations for the analysis of a seasonal fish-

ery is to correct the catch values to reflect the assumption of a constant fishing mortality rate ( $F$ ). The catch matrix for VPA would no longer contain the observed numbers of fish caught, but rather the numbers of fish that would have been caught under the assumption of an annual  $F$ . This paper presents a simple method for this conversion along with examples of the reduction of bias due to the method and a discussion of further applications. The Fortran source code and the executable program for this correction process are available from the authors.

## Methods

The algorithm for correcting annual catches from seasonal fisheries to meet the assumption of a constant fishing mortality rate during the year is as follows:

- Let  $i = 1, 2, \dots, K$  index time intervals (not necessarily of equal length) during the year;
- $\Delta t_i$  = the length of time in years for interval  $i$ ;
- $M$  = annual natural mortality rate;
- $C_i$  = observed catch in numbers during interval  $i$ ;
- $N_i$  = population numbers at the start of interval  $i$ ;
- $F_i$  = fishing mortality rate during interval  $i$ ; and
- $F_A$  = annual fishing mortality rate.

For each year, age cell in the VPA catch matrix:

- 1 Assume a value for  $N_{K+1}$ .
- 2 For each time interval progressing backwards from  $K$  to 1.
- 2a Solve for  $F_i$  given  $C_i$ ,  $N_{i+1}$ ,  $M$ , and  $\Delta t_i$  from the catch equation:

$$C_i = \frac{N_{i+1} e^{M\Delta t_i + F_i} F_i (1 - e^{-M\Delta t_i - F_i})}{M\Delta t_i + F_i}.$$

- 2b Compute  $N_i$  given  $N_{i+1}$ ,  $M$ ,  $\Delta t_i$  and  $F_i$  from the exponential decline equation:

$$N_i = N_{i+1} e^{M\Delta t_i + F_i}.$$

- 3 Compute  $F_A$  that reduces  $N_1$  to  $N_{K+1}$  given  $M$  as

$$F_A = -M - \ln \left[ \frac{N_{K+1}}{N_1} \right].$$

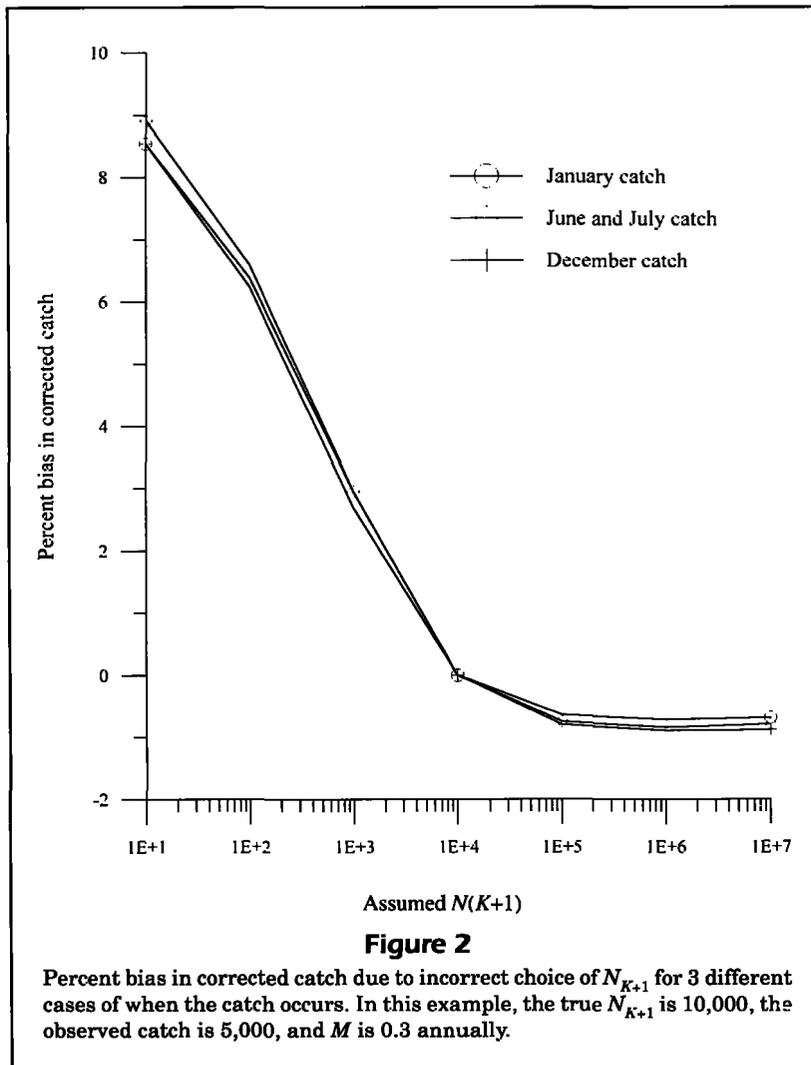
- 4 Compute annual catch ( $C_A$ ) under  $F_A$ , given  $N_1$  and  $M$  from catch equation:

$$C_A = \frac{N_1 F_A (1 - e^{-M - F_A})}{M + F_A}.$$

$C_A$  is the corrected catch to be used in VPA for the given year and age. Once all years and ages in the catch matrix have been corrected, the population abundance matrix can be estimated through virtual population analysis with the corrected catch values in place of the observed catches. The resulting population abundances at the end of the year can be used as the assumed values for  $N_{K+1}$  in step 1 and the process repeated to generate a recorrected catch matrix. Note that the observed catches are still used in step 2a of the algorithm; it is only the  $N_{K+1}$  values that change from computing the corrected to computing the recorrected catch. The recorrected catch matrix can again be used in virtual population analysis to estimate the population abundance matrix, and this iterative procedure can be repeated until the corrected catches do not change value.

This iterative process will produce population numbers from virtual population analysis that are consistent with the assumption of a constant fishing mortality rate during the year. Each annual catch in the VPA matrix is treated individually for the correction and then all the corrected catches used as input for VPA. The purpose for the iteration is to give a more solid basis for the choice of  $N_{K+1}$  for each observed catch (step 1 in algorithm) because the corrected catch value depends on the choice of  $N_{K+1}$  (Fig. 2). Guessing too high a value for  $N_{K+1}$  results in an underestimation of the corrected catch and vice versa, although, in general, the magnitude of bias is less for choosing  $N_{K+1}$  too large than too small. The timing of the catch also impacts the amount of bias in the corrected catch; earlier catches are slightly less biased than later catches (Fig. 2). The high biases found with low guesses for  $N_{K+1}$  correspond to extremely high values of the fishing mortality rate (Fig. 3, top panel) and are due to the catch removing a large portion of the population (>90%). When the catch is not removing such a large proportion of the population, a wide range of guesses for  $N_{K+1}$  will result in similar corrected catches (Fig. 3, bottom panel). The direction of the change between observed and corrected catch depends more upon the time of the catch than the  $N_{K+1}$  though (Fig. 4). It should be noted that the apparent linear relationship between corrected catch and time of the catch shown in Figure 4 is due to the values of  $N_{K+1}$  and  $M$  used in the example and will not always occur. The use of VPA results for values of  $N_{K+1}$  ensures a reasonable corrected catch value.

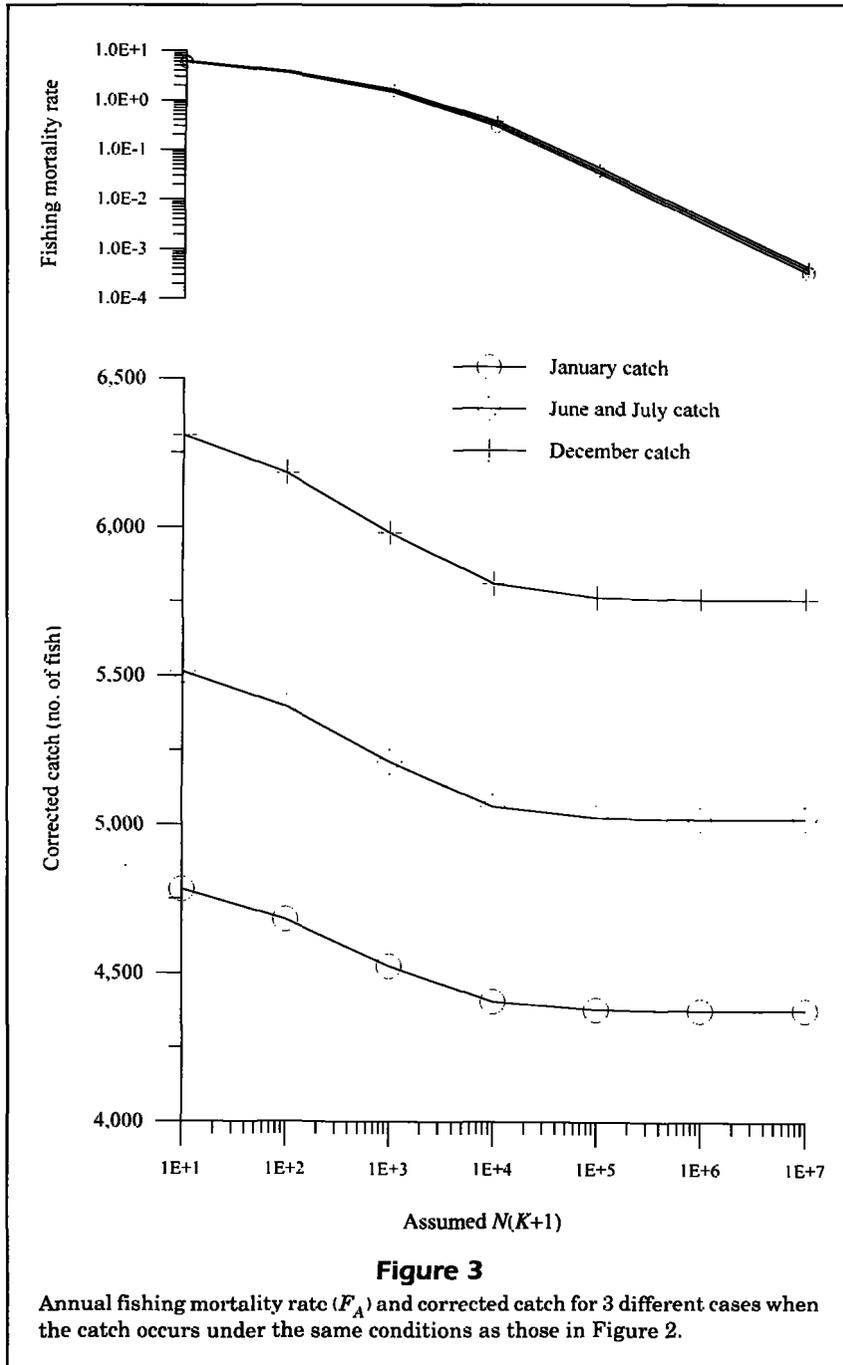
Once a value of  $N_{K+1}$  is chosen for an age cell of a given year in the VPA catch matrix, either from a



guess or from results of VPA, the corrected catch can be computed from the observed catch, the time sequence of the accumulation of this observed catch, and the natural mortality rate. Each cell in the catch matrix can have its own timing pattern. For example, if two gears operate in the fishery during different times of the year and target different-size fish, the timing of the catch will be different among ages. The observed catch for each time interval ( $C_i$ ) is used to solve for the fishing mortality rate during the interval ( $F_i$ ), given the population numbers at the start of the next interval ( $N_{i+1}$ ), the annual natural mortality ( $M$ ), and the length of the time interval ( $\Delta t_i$ ) (step 2a of the algorithm). The fishing mortality rate cannot be solved for directly in the equation and thus a search routine or iterative solution must be employed. A simple bisection algorithm will suffice, although quicker methods are available (see e.g. Press et. al., 1989). Once the fishing mortality rate for the

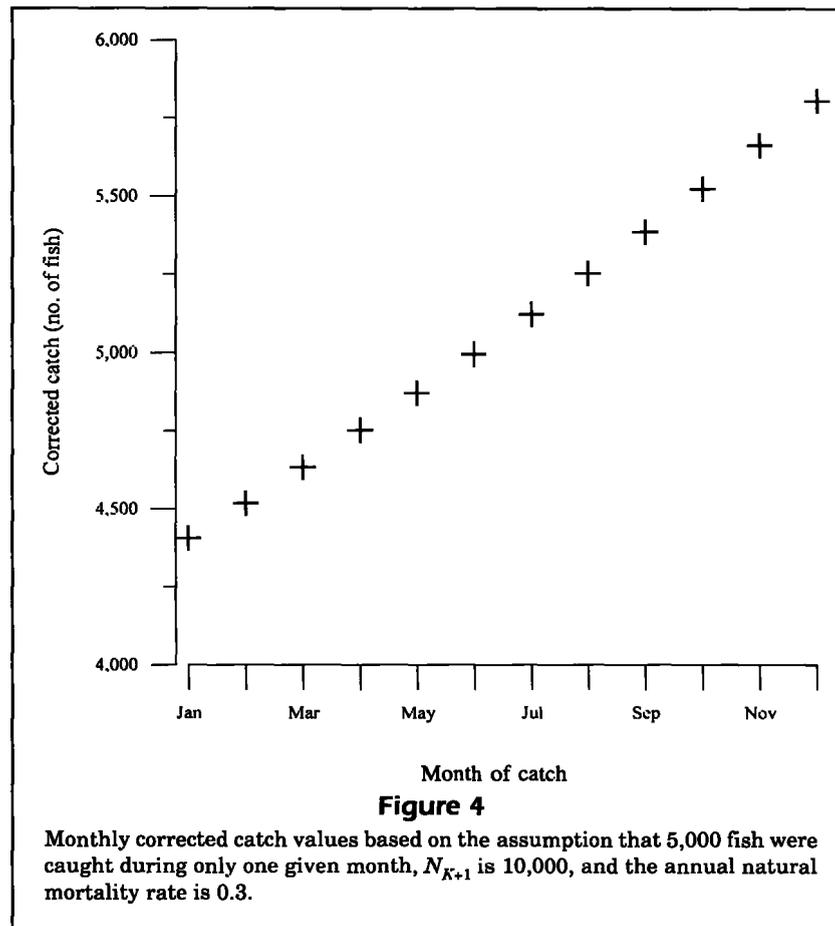
time interval ( $F_i$ ) is estimated, the population size at the start of the time interval ( $N_i$ ) can be computed directly with the equation in step 2b of the algorithm. Thus the natural and fishing mortality rates are assumed constant during each time interval, and the year should be split into time intervals accordingly. In most cases, monthly time steps should be sufficient unless the fishing season is extremely short and intense or the natural mortality rate is extremely high (or both situations occur).

The algorithm progresses backwards in time, from 31 December to 1 January, to minimize the propagation of errors, in the same manner that virtual population analysis follows a cohort backwards in time (Pope, 1972). When all the time intervals are completed, the corresponding annual fishing mortality rate ( $F_A$ ) can be computed from the equation given in step 3 of the algorithm. The population size at the start of time interval  $K+1$  is equivalent to the popu-



lation size for that cohort at the start of the next year and thus the annual  $F$  will reduce  $N_1$  to  $N_{K+1}$ . The annual  $F$  is then applied in the catch equation to generate the corrected catch ( $C_A$ ) (step 4 in the algorithm). The resulting catch is distributed throughout the year according to a constant  $F$  and thus reflects a smooth population abundance decline (see Figs. 5 and 6). In both Figures 5 and 6, the sum of the observed monthly catches are different from

the sum of the corrected monthly catches, whereas the observed and corrected population numbers follow different paths to the same endpoint. Figures 1 and 5 have the same observed catch, but the population numbers (and resulting fishing mortality rates) under the assumption inherent in the catch equation are different owing to the corrected catch value used in Figure 5. It is exactly the nonalignment of endpoints in Figure 1 that causes the bias in virtual



population analysis when catches from seasonal fisheries are used directly without correction.

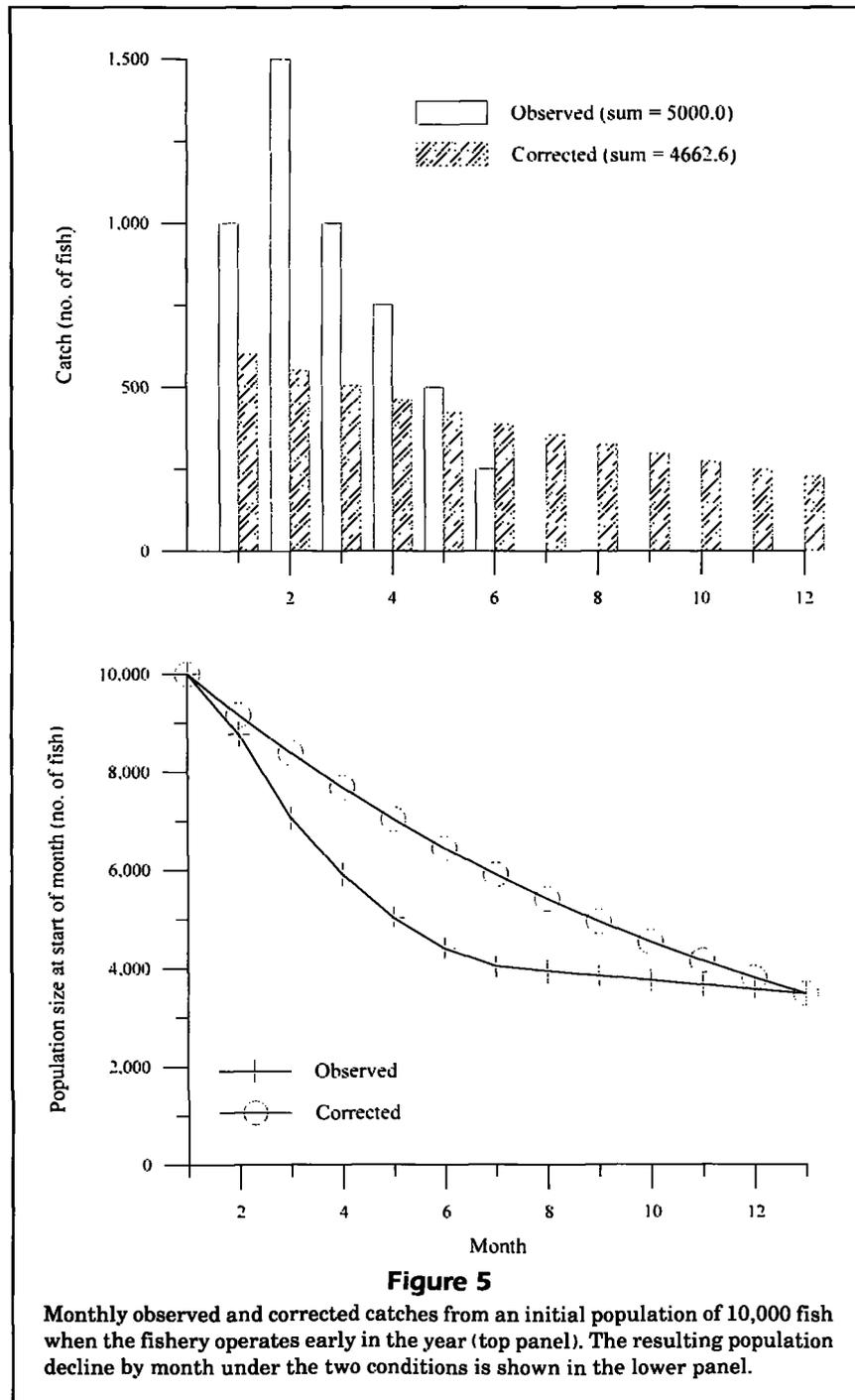
## Examples

Three scenarios were examined by means of simulation to demonstrate the algorithm. An initial population structure and recruitment pattern were set, and a given catch was removed at a constant fishing mortality rate under three scenarios: 1) the catch occurred only in January, 2) the catch was split evenly between June and July, and 3) the catch occurred only in December. The natural mortality rate was constant for all ages and years at 0.5 per year. The selectivity curve was sigmoid to follow a trawl-type pattern. A tuning index was collected from the population without error for use in calibrated virtual population analysis (VPA). The VPA used in the examples was FADAPT3 (Restrepo<sup>1</sup>). Any sequential popula-

tion analysis program could be used for these simulated examples because of a lack of error distributions for the data. Seven years were simulated for each scenario by applying the catch during the appropriate month(s) and the observed catch at age recorded for each year. For each scenario, 3 different sets of catch data were used as input for the VPA: 1) the observed catch-at-age data, 2) the corrected catch-at-age data with guesses for the  $N_{K+1}$  values, and 3) the recorrected catch-at-age data with the population numbers at age taken from the results of the corrected catch-at-age VPA. The resulting population numbers at age from the three VPA's were compared with the true values, and the percent bias in the estimates was computed. The true population numbers, 3 catch matrices, and 3 bias matrices are given for the January, June and July, and December catch scenarios in Tables 1, 2, and 3, respectively.

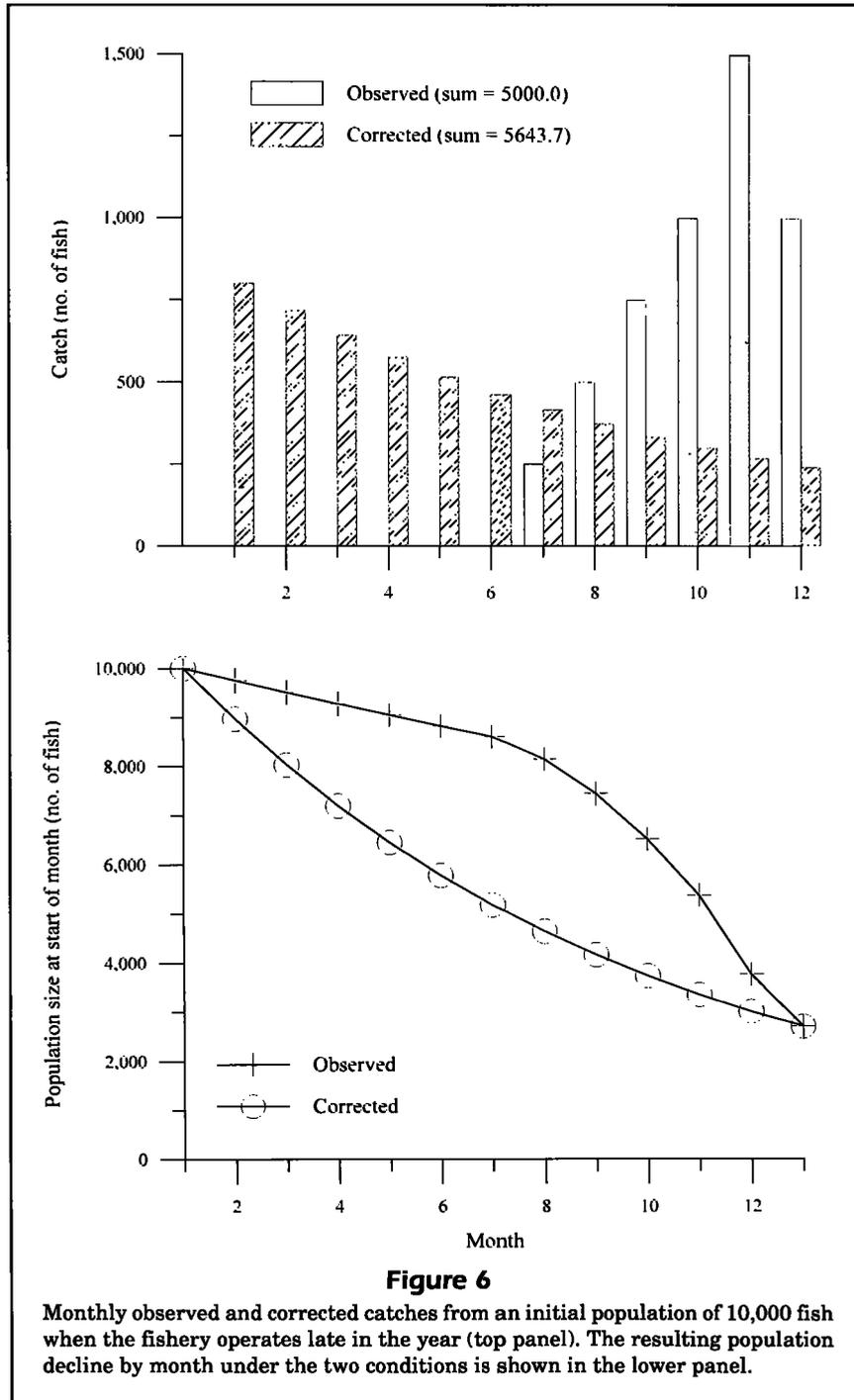
Although each scenario had the same initial population, recruitment pattern, and annual catches, the populations became quite different, depending upon when the catch was removed. The earlier the catch was taken in the year, the lower the resulting fishing mortality and the larger the remaining popula-

<sup>1</sup> Restrepo, V. 1996. Cooperative Unit for Fisheries Education and Research, Rosenstiel School of Marine and Atmospheric Science, Univ. Miami, 4600 Rickenbacker Causeway, Miami, FL 33149. Personal commun.



tion. The differences are most clearly seen in the older ages late in the simulated time span (Tables 1–3). The January catches were corrected to lower values than those of the observed catch, but the values for December corrected catches were higher than those for observed catches in order to reflect more accurately these changes in the fishing mortality rate caused by the timing of the catch.

In each scenario the recorrected catch matrix gave the lowest bias in estimated population size, whereas the observed catch resulted in the highest bias in two of the three scenarios (Table 4). The bias was largest for the observed catches that occurred in January and December. Use of observed January catches in the VPA overestimated the true population size, and use of observed December catches un-



derestimated the true population size. The June and July observed catches produced low bias, demonstrating the validity of Pope's cohort analysis approximation (Pope, 1972). The increasing bias at age for all three scenarios with corrected catch data was due to a choice of a small constant  $N_{K+1}$  value for all ages and years. This method of choosing  $N_{K+1}$  is not recommended during normal application of the algo-

rithm but was done to demonstrate the increased or decreased bias relative to observed catches, depending upon the timing of the catch. Much better guesses of  $N_{K+1}$  for the corrected catch would be the results of VPA with the observed catch matrix. In this case the re-corrected catches will usually be so similar to the corrected catches that no further iterations are required.



given an observed catch of 5,000 fish caught during January, June and July, or December and with a constant  $N_{K+1}$  of 10,000 fish. The resulting annual fishing mortality rates are also plotted in Figure 7 (top panel). The January corrected catches decrease in a

linear fashion over the range of  $M$ , and the associated fishing mortality rates decline rapidly as well. This decline occurs because the natural mortality rate has almost the entire year to change the population before the backward solution reaches Janu-

**Table 2**

True population numbers, observed catch, corrected catch, recorrected catch, and percent bias in population numbers output by VPA with the three catch matrices as input for scenario 2. Catch was split evenly between June and July. Years are in columns and ages are in rows.

Catch data for June and July							
<b>True population numbers</b>							
1,000,000	2,000,000	4,000,000	1,000,000	3,000,000	1,000,000	1,000,000	
563,368	498,972	1,041,839	2,134,702	552,040	1,652,398	521,608	
288,839	252,606	239,144	518,374	1,119,232	288,431	793,570	
144,699	110,580	107,036	107,278	251,844	540,885	122,597	
77,637	55,140	46,687	47,870	52,003	121,428	229,079	
<b>Observed catch</b>							
138,043	219,803	374,142	69,946	214,613	108,991	118,816	
114,430	81,561	145,831	225,396	59,580	267,951	91,865	
83,072	59,363	48,549	80,383	177,254	67,275	199,969	
41,948	26,205	21,918	16,786	40,244	127,221	31,148	
22,507	13,067	9,560	7,490	8,310	28,561	58,202	
<b>Corrected catch</b>							
143,534	230,844	398,149	71,908	225,269	112,829	123,191	
118,562	84,035	151,797	236,857	61,124	282,745	94,826	
85,615	60,898	49,689	82,802	185,260	69,126	209,559	
42,869	26,679	22,289	17,046	41,111	132,074	31,750	
22,892	13,257	9,689	7,586	8,419	29,094	59,693	
<b>Recorrected catch</b>							
140,605	223,496	380,043	70,958	217,723	110,825	120,889	
117,055	83,215	148,562	229,120	60,579	273,342	93,820	
85,518	60,869	49,670	81,973	180,784	68,986	205,317	
43,193	26,875	22,427	17,120	41,056	130,466	31,998	
23,177	13,402	9,783	7,640	8,478	29,296	59,785	
<b>% bias in population numbers from observed catch</b>							
-2.1	-2.0	-2.1	-2.1	-2.1	-1.7	-1.4	
-2.2	-2.1	-2.1	-2.1	-2.2	-2.2	-1.8	
-2.4	-2.2	-2.1	-2.1	-2.2	-2.3	-2.2	
-2.4	-2.2	-2.1	-2.1	-2.2	-2.3	-2.2	
-2.4	-2.2	-2.1	-2.1	-2.2	-2.3	-2.2	
<b>% bias in population numbers from corrected catch</b>							
-1.0	-0.9	0.0	-2.1	-0.2	-2.3	-2.4	
-1.1	-1.7	-1.5	-0.7	-2.4	-0.6	-2.9	
-1.4	-1.9	-2.4	-2.4	-1.3	-3.0	-1.7	
-1.9	-2.3	-2.7	-3.3	-3.2	-2.2	-4.3	
-2.4	-2.7	-3.1	-3.5	-4.0	-4.1	-3.8	
<b>% bias in population numbers from recorrected catch</b>							
0.1	0.1	0.1	0.1	0.1	0.0	0.0	
0.1	0.1	0.1	0.1	0.1	0.1	0.0	
0.1	0.1	0.1	0.1	0.1	0.1	0.1	
0.1	0.1	0.1	0.1	0.1	0.1	0.2	
0.1	0.1	0.1	0.1	0.1	0.2	0.1	

Table 3

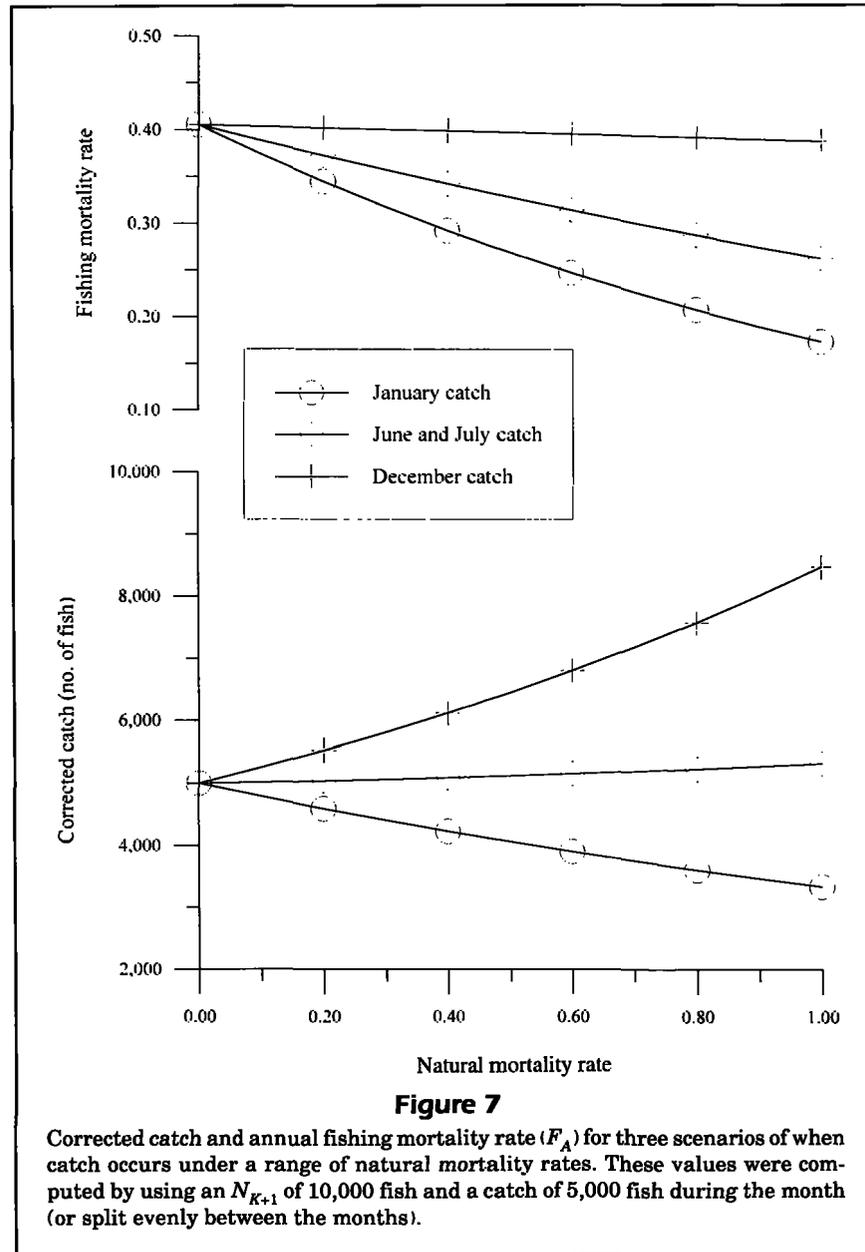
True population numbers, observed catch, corrected catch, rechecked catch, and percent bias in population numbers output by VPA with the three catch matrices as input for scenario 3. Catch occurred only in December. Years are in columns and ages are in rows.

Catch data for December							
True population numbers							
1,000,000	2,000,000	4,000,000	1,000,000	3,000,000	1,000,000	1,000,000	
563,368	468,980	986,837	2,044,458	532,809	15,944,22	489,054	
288,839	229,497	206,672	459,258	1,014,679	263,412	693,044	
144,699	95,547	85,574	83,737	205,232	450,766	96,185	
77,637	47,574	35,453	34,531	37,305	90,887	163,755	
Observed catch							
140,582	231,169	389,959	75,314	230,032	120,048	137,635	
114,731	79,510	142,362	230,269	61,058	280,134	97,654	
81,495	54,848	42,555	74,950	168,329	65,040	192,120	
41,126	23,014	17,764	13,784	34,340	112,163	26,861	
22,066	11,459	7,360	5,684	6,242	22,615	45,731	
Corrected catch							
184,448	306,692	524,132	97,697	305,147	157,007	180,502	
149,922	103,228	186,832	305,469	78,960	373,391	127,228	
105,848	70,827	54,785	97,218	221,702	84,184	253,787	
52,927	29,468	227,09	17,598	44,113	146,503	34,433	
28,246	14,619	9,376	7,237	7,949	28,953	58,922	
Rechecked catch							
180,390	296,049	498,706	96,173	293,745	153,805	176,580	
148,011	102,273	182,738	294,826	78,198	360,493	125,966	
105,966	71,003	54,919	96,365	216,452	84,285	249,728	
53,491	29,800	22,930	17,726	44,172	145,367	34,941	
28,703	14,838	9,500	7,310	8,030	29,319	59,482	
% bias in population numbers from observed catch							
-22.3	-22.3	-22.3	-22.4	-22.4	-21.9	-21.5	
-22.5	-22.4	-22.4	-22.4	-22.5	-22.5	-21.9	
-22.8	-22.6	-22.5	-22.5	-22.6	-22.7	-22.6	
-22.8	-22.6	-22.5	-22.5	-22.6	-22.7	-22.6	
-22.8	-22.6	-22.5	-22.5	-22.6	-22.7	-22.6	
% bias in population numbers from corrected catch							
-0.4	-0.1	0.9	-1.5	0.6	-1.3	-1.1	
-0.6	-1.2	-0.9	0.1	-1.9	0.2	-2.1	
-1.2	-1.6	-2.0	-1.8	-0.7	-2.5	-1.2	
-1.8	-2.1	-2.4	-2.9	-2.8	-1.9	-4.1	
-2.3	-2.5	-2.7	-3.1	-3.7	-3.8	-3.6	
% bias in population numbers from rechecked catch							
0.0	0.1	0.0	0.1	0.0	0.0	0.0	
0.0	0.1	0.1	0.1	0.1	0.1	0.1	
0.1	0.1	0.1	0.1	0.1	0.1	0.1	
0.1	0.1	0.1	0.1	0.1	0.1	0.1	
0.1	0.1	0.1	0.1	0.1	0.1	0.1	

ary and the catch occurs. Larger  $M$  will cause a large population size to be present at the start of February, and thus the fishing mortality rate needed to generate a given catch will be lower. In contrast, the December fishing mortality rates are nearly constant

over the range of  $M$  because the value of  $M$  does not change the population-size value used in step 2 of the algorithm as it did for the January catch.

These examples assume a constant natural mortality rate, which may be false in reality. If  $M$  varies dur-



ing the year, then the expected amount of bias removed by the catch correction algorithm may in fact be incorrect. The actual amount of bias between the true state of the population and the estimated values also depends upon the amount and type of error in the observed catch estimates and tuning indices. The reduction in bias produced by this algorithm may be insignificant relative to the level of bias produced by other sources in the analysis, but it should at least be in the correct direction.

The direction of change between observed and corrected catches has implications for quota projections and biological reference-point determination, such as  $F_{0.1}$  or  $F_{\%SPR}$ . Catches from early in the year are

corrected to lower values than those for the observed catch, and thus use of the observed catch in VPA results in overestimates of the population size, if unbiased indices are used to tune the VPA. The overestimated population size would then be used to predict a quota for the upcoming year which would be too large. When this quota was filled, observed catch, which is larger than the corrected catch in the VPA, would again be used in the following year's stock assessment and would thus predict a larger population size than was present. This feedback cycle could cause problems if the tuning indices do not adequately reflect the decline of the population.

**Table 4**

Unweighted average percent bias in population numbers for the three scenarios when catch occurs and the three catch matrices input in VPA (summary of Tables 1, 2 and 3).

Catch matrix	January	June and July	December
Observed	23.4	-2.1	-22.5
Corrected	-2.7	-2.2	-1.7
Recorrected	0.1	0.1	0.1

The determination of current stock health in relation to a biological reference point will also be affected by the timing of the catch, especially spawning potential ratios. If the catch is taken before spawning, a much lower spawning potential ratio will result in relation to the catch being taken after spawning (compare observed population numbers for June in Figures 5 and 6). Thus the timing of the catch must be incorporated into the prediction or reference point algorithms, whereas the population numbers at the start of the year can be derived from annual VPA's or from other techniques when the constant  $F$  is assumed, if the corrected catch values are input.

All the examples and discussion so far have been in terms of numbers of fish, but the quotas used by management are most often given in weight. The average weight at age for the catch and population has a confounding effect on the correction algorithm that can either reduce or increase the bias. The use of average weight of a fish at the midpoint of the year, combined with the assumption of a constant fishing mortality rate, can lead to highly biased quotas in relation to the true timing of the catch and the average weight at age of the fish at that time. A quota in weight, for fish caught early in the year, will cause more fish to be caught than the same quota filled late in the year when the fish have increased in weight. Thus particular attention must be paid to the growth of the fish during the year in relation to the timing of the catch in cases where management advice is based on weight data.

## Summary

Use of observed catch values from seasonal fisheries directly in virtual population analysis or in other

analyses, where a constant annual fishing mortality rate is assumed, will bias the population-size estimates. If the catch occurs at the beginning of the year, the population size will be overestimated, whereas catch late in the year will cause underestimation of the population size. The observed catches can be easily corrected to reflect the assumption of a constant fishing mortality rate and to eliminate bias through the algorithm presented in this paper.

## Acknowledgments

This manuscript benefited greatly from comments provided by V. Restrepo, J. Powers, D. Sampson, and two anonymous reviewers.

## Literature cited

- Hiramatsu, K.**  
1995. A theoretical study of equations used in virtual population analysis. *Fish. Sci. (Tokyo)* 61:752-754.
- MacCall, A. D.**  
1986. Virtual population analysis (VPA) equations for nonhomogeneous populations, and a family of approximations including improvements on Pope's cohort analysis. *Can. J. Fish. Aquat. Sci.* 43:2406-2409.
- Mertz, G., and R. A. Myers.**  
1996. An extended cohort analysis: incorporating the effect of seasonal catches. *Can. J. Fish. Aquat. Sci.* 53:159-163.
- Pope, J. G.**  
1972. An investigation of the accuracy of virtual population analysis using cohort analysis. *Int. Comm. Northwest Atl. Fish. Res. Bull.* 9:65-74.
- Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling.**  
1989. Numerical recipes: the art of scientific computing (FORTRAN version). Cambridge Univ. Press, New York, NY, 702 p.
- Sims, S. E.**  
1982. The effect of unevenly distributed catches on stock-size estimates using virtual population analysis (cohort analysis). *J. Cons. Cons. Int. Explor. Mer* 40(1):47-52.
- Ulltang, Ø.**  
1977. Sources of errors in and limitations of virtual population analysis (cohort analysis). *J. Cons. Cons. Int. Explor. Mer* 37(3):249-260.
- Youngs, W. D.**  
1976. An analysis of the effect of seasonal variability of harvest on the estimate of exploitation rate. *Trans. Am. Fish. Soc.* 105:45-47.