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Linearization with ordinary least-squares estimation, and nonlinear estimation of mortality using the catch equation

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The catch equation and mortality equation together give accumulated catch during a period of time in terms of recruitment R, the instantaneous fishing mortality coefficient F, and the instantaneous total mortality coefficient Z. The solution of the coupled equations can be linearized for estimation of Z by least squares, or it can be applied directly for nonlinear least-squares estimation of Z. Both approaches are applied to several populations. The two types of estimates can differ considerably. In general, linearization gives estimates of Z that best predict the logarithm of abundances, and nonlinear least squares gives estimates of Z that best predict abundances. Nonlinear estimates are best for calculation of yields.

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Introduction

Although cohort analysis is now widely applied for estimation of fishing mortalities, the method requires extensive data and an estimate of natural mortality, so in some situations catch-curve analysis is still useful. In catch-curve analysis, the equation

$$dN/dx = -ZN \tag{1}$$

is applied to model mortality, where N is the number of individuals in the population of a particular age, x is age, and Z is the total instantaneous mortality coefficient (e.g., Beverton and Holt, 1957).

Solution of Equation (1) gives the survival equation $N(x) = R\exp[-Z(x-x_r)]$, where N(x) is the number of individuals in the population of age x, R is the number of recruits, and x_r is age at recruitment. The solution can be linearized by taking the logarithm of both sides to give $\ln N(x) = \ln R - Z(x-x_r)$. Data available for fisheries are usually annual catch per unit of effort and not abundances, but Beverton and Holt (1957) showed that if the catchability coefficient q and fishing effort E are constant, and if we asume catch per unit of effort is proportional to abundance, the solution of Equation (1) becomes $C(x) = C(x_r)\ \exp[-Z(x-x_r)]$, where C(x) is catch of age x fish. This equation can also be linearized, but it deals with catch, not abundance or c.p.u.e., and available data are catches accumulated over a period of time. Beverton and Holt (1957) use moments to show accumulated catch also can be applied, but a simpler and more direct approach is possible.

Estimation of Z using the catch equation

To model mortality using catch data it is simple to model directly catch as well as mortality. This gives the coupled equations

$$dC/dx = FN \tag{2}$$

$$dN/dx = ZN \tag{3}$$

where F is the instantaneous fishing mortality coefficient. Solution of (3) gives the equation for abundance as a function of age; substitution into the equation for catch, Equation (2), and integration over some period of time such as a year gives the accumulated catch C_x during this period as

$$C_x = \frac{FR[1-\exp(-Z)]}{Z}\exp[-Z(x-x_r)]. \tag{4}$$

Equation (7) can also be linearized, the linear form being

$$\ln C_x = \ln\left[\frac{FR[1-\exp(-Z)]}{Z}\right] - Z(x-x_r). \tag{5}$$

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Equation (5) is the equation fitted when the logarithm of accumulated catch is regressed on age. In Equation (5) accumulated catch for the year of recruitment, x_r to $x_r + 1$, is given as $FR[1 - \exp(-Z)]$, and catches for older ages are calculated from this initial accumulated catch. Equation (5) is similar to that used for cohort analysis, but in cohort analysis integration of the catch equation is carried out over the entire exploited lifetime of the stock (Gulland, 1977). Equations (4) and (5) give explicitly the relations between the parameters F, R, Z, and the least-squares parameter estimates. Equation (4) can be used to estimate the product FR as well as Z, but F and R cannot be separated.

Gulland (1969) and Sandland (1982) have used an equation similar to (7) for estimation of natural mortality in mark and recapture studies. In this case R is the number marked and released, and is known, while C_x is the number of marked fish recaptured during sample period x. In mark and recapture regressions the variance of the dependent variable is not constant, for C_x is a binomial random variable with variance $n_x P_x(1 - P_x)$ where n_x is the number of fish caught during sample period x, and P_x is the probability of capture for marked fish. Gulland (1969) did not apply a weighted regression, but Sandland (1982) correctly indicates that in mark and recapture experiments a regression weighted by the inverse of the variance is necessary. Paloheimo (1963) developed a similar single mark and multiple recapture regression model, and applied weighted regression for estimation of the initial population size and its confidence interval.

Nonlinear estimation

Nonlinear least-squares estimates of the parameter Z and the product of the parameters F and R can be found using Equation (4); these are values of the parameters that minimize the residual sum of squares

$$\sum_{x=0}^{n} (C_x - \hat{C}_x)^2, \tag{6}$$

where C_x is the observed catch for age x, $\hat{C}_x$ is the catch for age x calculated using Equation (4) and the parameter estimates, and n is the number of age groups. In linearization followed by regression the equation fitted is

$$C_x = \frac{FR[1 - \exp(-Z)]}{Z} \exp[-Z(x - x_r) + e_x] \tag{7}$$

where e_x is an error term, and in nonlinear regression the equation fitted is

$$C_x = \frac{FR[1 - \exp(-Z)]}{Z} \exp[-Z(x - x_r)] + e_x. \tag{8}$$

The error term is entered differently in these two equations, and the estimates of Z for the two approaches can be different.

Application

Both methods for estimation of Z were applied to several species of fish (Table 1). All estimates were made using SYSTAT (Wilkinson, 1987). Sometimes the two estimates of the mortality coefficient were different, and sometimes they were close (Table 1); there was no pattern. Sometimes linearization followed by regression

Table 1. Catch-at-age data, nonlinear (NL) and linearization (LS) estimates of Z, and standard errors of the estimates of Z for several different fisheries.

Age $(x-x_r)$	Cod[a]	Plaice[b]	Smallmouth bass[c]	Pacific herring[d]	English sole[e]
0	12862	1670	89	2607	138
1	8995	951	18	497	77
2	6549	548	5	91	27
3	3240	316	2	17	11
4	3005	180	–	4	3
5	1566	105	–	1	–
6	1442	–	–	–	–
7	1199	–	–	–	–
Z_{LS}	0.36	0.56	1.24	1.58	0.96
SE(LS)	0.0269	0.001	0.07	0.026	0.052
Z_{NL}	0.385	0.557	1.51	1.66	0.739
SE(NL)	0.022	0.002	0.056	0.004	0.073

[a]Average catch of West Greenland cod (*Gadus morhua*) (Schumacher, 1971).
[b]Catch of plaice (*Pleuronectes platessa*) landed at Lowestoft per 100 hours of fishing (Gulland, 1969).
[c]Catch of smallmouth bass (*Micropterus dolomieui*) in northern Lake Michigan (Latta, 1975).
[d]Catch of Pacific herring (*Clupea harengus pallasi*) off British Columbia (Tester, 1955).
[e]Catch of English sole (*Parophrys vetulus*) off Strait of Georgia (Ricker, 1958; he called the species lemon sole).

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Table 2. Observed age structures (OBS) and age structures predicted using the least-squares (LS) and nonlinear (NL) estimates of Z for species where the estimates were different.

Age ($x-x_r$)	Smallmouth bass			Pacific herring			English sole		
	NL	LS	OBS	NL	LS	OBS	NL	LS	OBS
0	83.94	72.24	84	2607.17	2351.95	2607	140.78	169.53	138
1	18.56	20.72	18	495.72	482.03	497	67.24	64.91	77
2	4.10	5.94	5	94.26	98.79	91	32.11	24.85	27
3	0.91	1.70	2	17.92	20.25	17	15.34	9.52	11
4	–	–	–	3.41	4.15	4	7.32	3.64	3
5	–	–	–	0.65	0.85	1			

Table 3. Logarithms of observed age structures (OBS) and logarithms of age structures predicted using the least-squares (LS) and nonlinear (NL) estimates of Z for English sole.

Age ($x-x_r$)	English sole		
	NL	LS	OBS
0	4.947	5.133	4.927
1	4.208	4.173	4.343
2	3.469	3.213	3.295
3	2.730	2.253	2.397
4	1.991	1.293	1.098

was more precise than nonlinear least squares, and sometimes nonlinear least squares was more precise than linearization, but again there was no pattern (Table 1).

However, for younger ages in the recruited stock, predictions of age structure made with nonlinear estimates of Z were always closer to the observed age structure than were predictions made with linearization estimates of Z (Table 2). The reason for this difference is clear when the logarithms of catch and predicted catch are examined. The errors in predicted catches of younger age groups using the linearization estimate of Z are largest for English sole, and the errors are large compared with those for predictions made using the nonlinear estimate of Z (Table 2).

The errors in prediction of the logarithm of catches are relatively small for the linearization estimate of Z (Table 3). In linearization the logarithm of catch is fitted, whereas in nonlinear estimation the catch itself is fitted, and a model that predicts the logarithm of catches well does not always predict catches well. For yield estimation, especially when the total mortality rate is high, the younger age groups in the recruited stock are most important because these age groups are most abundant; in such situations nonlinear regression estimates of mortality give the most accurate description of mortality for yield assessment.

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