

THE USE OF AUXILIARY VARIABLES IN
CAPTURE-RECAPTURE AND REMOVAL EXPERIMENTS

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SUMMARY

The dependence of animal capture probabilities on auxiliary variables is an important practical problem which has not been considered when developing the statistical methodology of population estimation for capture-recapture and removal experiments. In this paper the linear logistic binary regression model is used to relate the probability of capture to continuous auxiliary variables. The auxiliary variables could be environmental quantities such as air or water temperature, or individual animal characteristics such as body length or weight. Maximum likelihood estimators of the population parameters are considered for a variety of models which all assume a "closed" population but this can easily be generalized to allow for recruitment. Testing between models is also considered. This model can also be used when the auxiliary variable is a measure of the effort expended in obtaining the sample.

Key words: Binary regression; Catch-Effort sampling; Capture-Recapture sampling; Removal method; Linear logistic regression model.

1. Introduction

There is a very large literature on the statistical methodology of capture-recapture and removal sampling with much of it concerned with building increasingly realistic models of the sampling processes involved in practical applications. In view of all this work it is surprising that no one has considered building a model relating capture probabilities to auxiliary variables despite strong evidence of their influence in real experiments (Perry, et al. 1977, Lagler 1968, Joule and Cameron 1974).

The auxiliary variables may be of two types:

(i) environmental -- These quantities affect all the animals at a particular sampling time. Examples would be air temperature, water temperature and humidity. Also another important example would be the amount of effort expended in obtaining the sample. (ii) animal -- These quantities affect an individual animal's probability of capture. Examples would be age, weight or body length. In this paper models are developed relating capture probabilities to both types of continuous auxiliary variables.

The problem being considered is basically a complex example of binary regression. A definitive reference on this topic is Cox (1970). The models developed are based on the linear logistic relationship (Cox 1970, p. 18). For example, suppose one had an auxiliary variable (x) to relate to a probability of capture (p) in a particular sample the relationship would be

$$p = \exp(\alpha + \beta x) / \{1 + \exp(\alpha + \beta x)\}$$

$$\text{or } \lambda = \log_e \{p/(1 - p)\} = \alpha + \beta x.$$

Here α and β are the parameters defining the relationship and λ is the logistic transform.

In §2 a series of models for environmental variables is developed. Maximum likelihood estimation of the population parameters is considered as well as testing between models. In §3 a series of models is developed when there is a variable (such as body weight) which characterizes each individual animal and which affects probability of capture. This is more complex than the problem considered in §2 because if we proceed directly then part of the likelihood is unobservable. To overcome this the variable is considered as a sequence of categories and within each category the probability of capture is assumed constant (for a particular sample).

In §4 a slightly different auxiliary variable is considered. This is the amount of effort expended in collecting the sample. There are various models in the literature relating the effort to the capture probability (Seber 1973, p. 296). Here we consider the model developed in §2 and show that it is a useful alternative model for this situation. In §5 we consider two detailed examples to illustrate the methodology taken from Paloheimo (1963). Finally there is a general discussion section.

2. Environmental Variables

2.1 Introduction and Notation

In this section we relate the capture probabilities for any sample in a K sample capture-recapture experiment to a set of continuous environmental variables using the linear logistic relationship. The models considered here are for a closed population of N animals and either have equal catchability or allow trap response of the animals in any sample. Specifically the two basic models considered here are:

H_0 : Equal Catchability Model

H_1 : Trap Response Model.

The following notation will be used in this section of the paper:
 N is the population size during the whole of the k-sample capture-recapture experiment.

n_i is the sample size of the i th sample $i = 1, \dots, k$.

$m_i(u_i)$ is the number of marked (unmarked) animals in the i th sample $i = 1, \dots, k$.

M_i is the number of marked animals in the population just before the i th sample $i = 1, \dots, k + 1$. This means that $M_i = \sum_{j=1}^{i-1} u_j$ with $M_1 = 0$ and $M_{k+1} = \sum_{j=1}^k u_j$.

$\{X_\omega\}$ is the vector of numbers of animals with all possible capture histories during the experiment.

Y_{ji} is the value taken by the j th environmental variable in the i th sample $j = 1, \dots, m$ and $i = 1, \dots, k$. For simplicity let us also define $Y_{0i} = 1$ for $i = 1, \dots, k$.

$c_i(p_i)$ is the probability of capture of the marked (unmarked) animals in the i th sample $i = 1, \dots, k$.

The linear logistic relationship defines

$$\log \{p_i / (1-p_i)\} = \sum_{j=0}^m \beta_j^{(u)} Y_{ji} = \underline{\beta}^{(u)'} \underline{Y}_i$$

and

$$\log \{c_i / (1-c_i)\} = \sum_{j=0}^m \beta_j^{(c)} Y_{ji} = \underline{\beta}^{(c)'} \underline{Y}_i$$

where $\underline{\beta}^{(u)}$, $\underline{\beta}^{(c)}$ are the vectors of parameters of the relationship for the unmarked and marked animals respectively.

2.2 H₀: Equal Catchability Model

In this case we assume all the animals have the same probability of capture in each sample ($p_i = c_i$ for $i = 1, \dots, k$ which implies $\beta_j^{(u)} = \beta_j^{(c)} = \beta_j$ for all $j = 0, 1, \dots, m$). The point probability of $\{X_\omega\}$ is then given by

$$\begin{aligned}
 P_{H_0} \left\{ \{X_\omega\}; N, \underline{\beta} \right\} &= \frac{N!}{\prod_{\omega} X_\omega! (N-M_{k+1})!} \prod_{i=1}^k p_i^{n_i} (1-p_i)^{N-n_i} \\
 &= \frac{N! \exp \left\{ \sum_{i=1}^k n_i \beta' \underline{Y}_i \right\}}{\prod_{\omega} X_\omega! (N-M_{k+1})! \prod_{i=1}^k \{1 + \exp(\beta' \underline{Y}_i)\}^N} \quad (1)
 \end{aligned}$$

The joint minimal sufficient statistic $(M_{k+1}, \sum_{i=1}^k n_i Y_{ji}; j = 0, 1, \dots, m)$ is of the same dimension ($m + 2$) as the parameters ($N, \beta_j; j = 0, 1, \dots, m$).

Maximum likelihood estimation involves iterative techniques and will be discussed in the Appendix. Under this model the parameters ($N, \beta_j; j = 0, 1, \dots, m$) are all identifiable provided m is less than or equal to $(k-1)$.

2.3 H₁: Trap Response Model

Here we relax the assumptions so that marked animals can have a different probability of capture from unmarked animals in any sample. The joint probability distribution of $\{X_\omega\}$ is now given by

$$P_{H_1} \left\{ \{X_\omega\}; N, \beta^{(u)}, \beta^{(c)} \right\} = \frac{N!}{\prod_{\omega} X_\omega! (N-M_{k+1})!} \prod_{i=1}^k p_i^{u_i} (1-p_i)^{N-M_i-u_i} c_i^{m_i} (1-c_i)^{M_i-m_i}$$

$$= \left[\frac{N! \exp\left(\sum_{j=0}^m \beta_j^{(u)} \sum_{i=1}^k u_i Y_{ji}\right)}{u_1! \dots u_k! (N-M_{k+1})! \prod_{i=1}^k \{1 + \exp\left(\sum_{j=0}^m \beta_j^{(u)} Y_{ji}\right)\}^{N-M_i}} \right]$$

$$\left[\frac{u_1! \dots u_k! \exp\left(\sum_{j=0}^m \beta_j^{(c)} \sum_{i=1}^k m_i Y_{ji}\right)}{\prod_{\omega} X_\omega! \prod_{i=1}^k \{1 + \exp\left(\sum_{j=0}^m \beta_j^{(c)} Y_{ji}\right)\}^{M_i}} \right] \quad (2)$$

The Removal Model

If all of the β parameters are distinct for the marked and unmarked animals then the marked animals give us no information about the population size (N). This means we may just consider the first term of (2) which is the joint distribution of the unmarked animals in each sample as our likelihood. Notice that this is the same model as would apply if the animals were removed permanently from the population, the so-called "Removal Model." We can find the maximum likelihood estimators and their asymptotic variance-covariance matrix as in the previous model. (See Appendix for details). For identifiability of all parameters m cannot exceed $k-2$.

The Full Trap-Response Model

If all the β parameters are the same for the marked and unmarked animals except for a different constant term ($\beta_j^{(u)} = \beta_j^{(c)} = \beta_j$ for $j=1, \dots, m$ but $\beta_0^{(u)} \neq \beta_0^{(c)}$) then we should use the full likelihood (2).

The marked animals are providing information useful in the estimation of N . Maximum likelihood estimation follows as before and for identifiability of all the parameters we once again require m to be less than or equal to $(k-2)$.

2.4 Testing Between Models

Let $\underline{\theta}$ be a vector of parameters defining the linear logistic relationship for any of the models considered in this section. It is possible to test this model against a more restrictive hypothesis $\underline{\theta}_0 \in \underline{\theta}$ by use of statistic

$$2 \{L(\hat{\underline{\theta}}, \hat{N}) - L(\underline{\theta}_0, \hat{N}_{(0)})\}$$

where $L(\cdot)$ is the log likelihood under each model. Subject to certain regularity conditions this statistic is asymptotically $\chi^2_{(v)}$ under the more restrictive hypothesis with v the difference in dimensionality of the parameter spaces under the two hypotheses (Kendall and Stuart 1973, p. 240). Darroch (1959) has shown that this asymptotic theory is valid for tests of this type in capture-recapture experiments.

3. Individual Animal Variables

3.1 Introduction and Notation

Here we assume the probability of capture of an animal is related to a "size" variable (age, length) by the linear logistic model. We assume a closed population and that the sampling experiment is short enough that the animal does not change size appreciably during the experiment.

To construct a useful model we have to categorize the population into l categories with animal numbers N_j for $j=1, \dots, l$ and midpoint size variable for the j th category Y_j for $j=1, \dots, l$. If we try and use the size measurement of each animal directly part of the likelihood is unobservable. This results from the fact that size measurements are unknown for the $(N - M_{k+1})$ animals which are never captured. Once again we consider the two basic models

H_0 : Equal Catchability Model

H_1 : Trap Response Model

as in §2.

The following notation which is slightly generalized over §2 is used in this section: -

N_j is the population size of the j th size class for $j=1, \dots, l$.

n_{ij} is the number of animals in the j th size class which are caught in the i th sample for $j=1, \dots, l$ and $i=1, \dots, k$.

$m_{ij}(u_{ij})$ is the number of marked (unmarked) animals in the j th size class which are caught in the i th sample for $j=1, \dots, l$ and $i=1, \dots, k$.

M_{ij} is the number of marked animals of the j th size class present in the population just before the i th sampling time for $j=1, \dots, l$ and $i=1, \dots, k$.

$\{x_{\omega j}\}$ is the vector of number of animals for all possible capture histories for the j th size class $j=1, \dots, l$.

Y_j is the midpoint size of the j th class for $j=1, \dots, l$.

3.2 H_0 : Equal Catchability Model

Under this model p_{ij} which is the probability of capture of any of the N_j animals belonging to the j th size class in the i th sample $j=1, \dots, l$ and $i=1, \dots, k$ is defined by the following relationship

$$\log \{p_{ij}/(1-p_{ij})\} = \alpha_i + \beta_i Y_j$$

and the joint distribution of the vector of all capture histories is given by

$$\begin{aligned}
 & P_{H_0} \{ \{ \chi_{\omega} \}; N_j, \alpha_i, \beta_i, i=1, \dots, k, j=1, \dots, \ell \} \\
 &= \prod_{j=1}^{\ell} P_{H_0} \{ \{ \chi_{\omega_j} \}; N_j, \alpha_i, \beta_i, i=1, \dots, k \} \\
 &= \prod_{j=1}^{\ell} \left\{ \frac{N_j!}{\prod_{\omega_j} X_{\omega_j}! (N_j - M_{(k+1)_j})!} \prod_{i=1}^k p_{ij}^{n_{ij}} (1-p_{ij})^{N_j - n_{ij}} \right\} \\
 &= \prod_{j=1}^{\ell} \frac{N_j!}{\prod_{\omega_j} X_{\omega_j}! (N_j - M_{(k+1)_j})!} \frac{\exp \left\{ \sum_{j=1}^{\ell} \sum_{i=1}^k (n_{ij} \alpha_i + n_{ij} \beta_i Y_j) \right\}}{\prod_{j=1}^{\ell} \prod_{i=1}^k \{ 1 + \exp(\alpha_i + \beta_i Y_j) \}^{N_j}}. \quad (3)
 \end{aligned}$$

For this model we have a $(2k+\ell)$ parameter space $\{N_j; j=1, \dots, \ell; \alpha_i, \beta_i; i=1, \dots, k\}$ and the minimal sufficient statistic for the model has the same dimension and is given by $\{M_{(k+1)_j}; j=1, \dots, \ell; \sum_{j=1}^{\ell} n_{ij}, \sum_{j=1}^{\ell} n_{ij} Y_j; i=1, \dots, k\}$. This is a straightforward generalization of the results in § 2.2. Maximum likelihood estimation can be tackled as in § 2.

An important special case of this model is where $\alpha_i = \alpha, \beta_i = \beta$ for $i = 1, 2, \dots, k$. That is in each size category there is a constant probability of capture for the whole experiment.

3.3 H_1 : Trap Response

Under this model we allow the marked animals to have a different probability of capture (c_{ij}) from the unmarked (p_{ij}) for each size class in each sample. The relationships are defined by

$$\log_e \{ p_{ij} / (1-p_{ij}) \} = \alpha_i^u + \beta_i^u Y_j$$

and

$$\log_e \{ c_{ij} / (1-c_{ij}) \} = \alpha_i^c + \beta_i^c Y_j.$$

Unfortunately for useful identifiable models we need to make the restrictions $\alpha_i^u = \alpha^u$, $\beta_i^u = \beta^u$, $\alpha_i^c = \alpha^c$ and $\beta_i^c = \beta^c$ for $i=1, \dots, k$.

If no further restrictions are made then this model is a generalization of the "Removal method" (§2.3) whereas if we make the further restriction that $\beta^c = \beta^u$ we are in a generalization of the "Full Trap Response Model" (§2.3). In both cases the likelihood inference is a straightforward generalization of results in §2.

4. A New Catch-Effort Model

The use of effort data as an auxiliary variable in removal sampling is very common especially in fisheries. Seber (1973, p. 296) discusses this problem in detail.

The standard model is based on the assumption that sampling is a poisson process with regard to effort. Thus the probability of capture in a sample (p) is related to the effort (f) expended in collecting the sample by $p=1-\exp(-\gamma f)$ with γ defined as the "catchability" coefficient. In practice (γf) is usually small and the equation simplifies to the approximate form

$$p \approx \gamma f \tag{4}$$

When (4) is valid then a plot of catch per unit of effort versus cumulative catch over the whole sampling experiment should be linear and a regression method of estimating N can be used (Seber 1973; p. 297).

An alternative **empirical** model is to use the linear logistic relationship

$$p = \exp(\beta_0 + \beta_1 f) / \{1 + \exp(\beta_0 + \beta_1 f)\}$$

with estimation of N following from the material of §2.3 because f is analogous to an environmental variable.

To illustrate the regression model and a series of logistic models:

- (i) $H_0: \lambda = \log_e \{p/(1-p)\} = \beta_0$, a constant probability of capture model; (ii) $H_1: \lambda = \log_e \{p/(1-p)\} = \beta_0 + \beta_1 f$, a linear logistic model

relating capture probability to effort; and (iii) $H_2: \lambda = \log_e \{p/(1-p)\} = \beta_0 + \beta_1 f + \beta_2 f^2$, a quadratic logistic model relating capture probability to effort, are fitted to a set of lobster data originally presented by De Lury (1947) and reanalyzed by Seber (1973, p. 299) (Table 1). The catch is in pounds rather than numbers and thus there is an approximation in using the multinomial model here.

(Table 1 to appear here)

In Table 2 the point and ninety-five percent confidence interval estimates for the population size are presented for all four models. The regression, linear (H_1) and quadratic models (H_2) all give similar point estimates but notice that the confidence interval for the regression model greatly exceeds those of the other models. This will be considered further in the discussion section.

(Table 2 to appear here)

In Table 3 a comparison of the expected catches under all four models is given. Notice that H_0 , the constant capture probability model, obviously fits much worse than the other three models. There is not much to choose between the other three models which all appear to fit the data adequately. However, none of the models fit the data based on a traditional chi-square goodness of fit test appropriate for multinomial distributions. Use of likelihood ratio tests for H_0 vs H_1 and H_1 vs H_2 showed the need for a quadratic term. However, as we have seen, the population size estimates did not change appreciably after the addition of the quadratic term. We consider the question of goodness of fit and choice of model further in the discussion section.

(Table 3 to appear here)

5. Examples

In this section we consider data on two Canadian lobster fisheries (Tignish 1951, Port Maitland 1950-51) taken from a paper by Paloheimo (1963). The data consist of number of "legal size" lobsters removed in a weekly period, the number of trap hauls in the period, and the average water (bottom) temperature ($^{\circ}\text{C}$) for the period. (See Tables 4 and 5).

(Tables 4 and 5 to appear here)

To illustrate the methodology developed in §2 we consider the following three logistic models for this data:

(i) $H_0: \lambda = \log_e \{p/(1-p)\} = \beta_0$, a constant probability of capture model;

(ii) $H_1: \lambda = \log_e \{p/(1-p)\} = \beta_0 + \beta_1 f$, a linear logistic model relating capture probability to effort;

(iii) $H_2: \lambda = \log_e \{p/(1-p)\} = \beta_0 + \beta_1 f + \beta_2 t$, a linear logistic model relating capture probability to effort and temperature.

In Tables 6 and 7 we present maximum likelihood estimates and their standard errors for each of the three models for the Tignish and Port Maitland data. In both cases the size of the regression coefficient for temperature ($\hat{\beta}_2$) relative to its standard error suggests that the temperature effect is important.

(Tables 6 and 7 to appear here)

In Tables 8 and 9 the expected values for the catch under the three models are compared with the observed catch first for the Tignish fishery and then the Port Maitland fishery. In both cases the constant capture

probability model (H_0) fits very poorly. In both cases there is a progressively better fit as you move from H_0 to H_1 to H_2 which is validated by significant likelihood ratio tests for H_0 vs H_1 and H_1 vs H_2 . We feel that for both data sets the model involving effort and temperature (H_2) is very good and is recommended to obtain population size estimates. However, it is also clear that the Port Maitland data fits the model much better than the Tignish data.

(Tables 8 and 9 to appear here)

Despite our feeling that model H_2 is a useful model to relate capture probability to effort and temperature for this lobster data we find that none of the models fit using chi-square goodness of fit tests. We discuss this further in the next section.

6. Discussion

The models developed in §2 relating capture probabilities to environmental variables could be very useful in practice. This is especially so in experiments where the animals are removed because then N is only identifiable if capture probabilities are related to each other to reduce the number of unknown parameters. The lobster data of Paloheimo (1963) which we considered in §5 gives a good illustration of the value of these models.

It is recommended that biologists measure environmental variables when carrying out their experiments. This has often not been done in the past so that it is difficult to obtain data to evaluate the models suggested here.

Concerning use of the linear logistic model for effort data there are advantages and disadvantages over the standard model. It is possible to fit a series of models of increasing complexity (§4) and compare fits using

approximate likelihood ratio tests. Also it is possible to easily incorporate other environmental variables into the model unlike the standard model. One disadvantage is that fitting linear logistic models requires iterative solution of maximum likelihood equations whereas for the standard model simple modifications of linear regression techniques can be used. Another disadvantage is that the linear regression technique obtains a variance estimate from the spread of the catch values about the regression line whereas the logistic models use a theoretical estimate of the variance based on asymptotic maximum likelihood theory. Therefore, the regression technique is able to account for variability due to day to day fluctuations in the capture probabilities. This explains the much larger variability of the regression estimate in the De Lury (1947) data (Table 2).

In removal studies the capture probabilities at each sampling time are assumed to remain constant except for changes directly induced by the measured auxiliary variables. In practice this is unlikely to be the case, there will always be some additional variability in capture probabilities due to unmeasured variables. This explains the rejection of the models by traditional chi-square goodness of fit tests (§4 and §5). Nevertheless, we feel that logistic models often produce an adequate fit to the data and should be used in practice as no other methods are available to estimate population size for removal studies.

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APPENDIX

Partial Derivatives

Model H₀

Under Model H₀ the first and second partial derivatives of the log-likelihood (L) based on (1) are given by

$$\frac{\partial L}{\partial \beta_j} = \sum_{i=1}^k Y_{ji} (n_i - Np_i),$$

$$\frac{\partial L}{\partial N} = \left(\frac{1}{N} + \frac{1}{N-1} + \dots + \frac{1}{N-M_{k+1}+1} \right) + \sum_{i=1}^k \log_e (1-p_i),$$

$$\frac{\partial^2 L}{\partial \beta_j \partial \beta_\ell} = -N \sum_{i=1}^k Y_{ji} Y_{\ell i} p_i (1-p_i),$$

$$\frac{\partial^2 L}{\partial \beta_j \partial N} = - \sum_{i=1}^k Y_{ji} p_i,$$

and

$$\frac{\partial^2 L}{\partial N^2} = - \left(\frac{1}{N^2} + \frac{1}{(N-1)^2} + \dots + \frac{1}{(N-M_{k+1}+1)^2} \right).$$

Here recall $p_i = \exp \left(\sum_{j=0}^m \beta_j Y_{ji} \right) / \left[1 + \exp \left(\sum_{j=0}^m \beta_j Y_{ji} \right) \right]$ and

the range of suffices being $i = 1, \dots, k$; $j = 0, 1, \dots, m$ and $\ell = 0, 1, \dots, m$.

Model H

Under the Removal Model which is a special case of Model H₁ the first and second partial derivatives of the log-likelihood (L) based on the first term of (2) are given by

$$\frac{\partial L}{\partial \beta_j(u)} = \sum_{i=1}^k Y_{ji} \left\{ u_i - (N-M_i)p_i \right\}$$

with $\frac{\partial L}{\partial N}$ as in Model H₀.

and

$$\frac{\partial^2 L}{\partial \beta_j(u) \partial \beta_\ell(u)} = - \sum_{i=1}^k (N-M_i) Y_{ji} Y_{\ell i} p_i (1-p_i)$$

with $\frac{\partial^2 L}{\partial \beta_j^{(u)} \partial N}$ and $\frac{\partial^2 L}{\partial N^2}$ as in Model H_0 .

Here recall $p_i = \exp \left(\sum_{j=0}^m \beta_j^{(u)} Y_{ji} \right) / [1 + \exp \left(\sum_{j=0}^m \beta_j^{(u)} Y_{ji} \right)]$

and the suffices of i , j and l are the same as under Model H_0 .

Maximum Likelihood Estimation

The maximum likelihood estimators have to be found iteratively using these partial derivatives. One approach is the Newton-Raphson procedure (Seber (1973; p. 17)). The asymptotic variance-covariance matrix can also be found as a by product of the method.

During the preparation of our numerical examples the second author (Hines) wrote a Fortran program "LINLOGN" for the removal model. This program computes maximum likelihood estimators for the two, three and four parameter logistic models we used. Hines found it useful to use a modified two stage version of the Newton-Raphson procedure because N is really a discrete parameter. Variances and covariances of the parameters are computed along with chi-square goodness of fit tests and likelihood ratio tests for distinguishing between the three nested models.

Table 1

Catch and effort data for a lobster population from
De Lury (1947) and reanalyzed by Seber (1973)

Date	i	Catch (n_i) ^a	Effort (f_i) ^a	Catch/Effort (n_i/f_i)	Cumulative Catch
May 23	1	6.995	8.470	0.8259	0
24	2	5.851	7.770	0.7530	6.995
25	3	3.221	3.430	0.9391	12.846
26	4	6.345	7.970	0.7961	16.067
27	5	3.035	4.740	0.6403	22.412
29	6	6.271	8.144	0.7700	25.447
30	7	5.567	7.965	0.6989	31.718
31	8	3.017	5.198	0.5804	37.285
June 1	9	4.559	7.115	0.6408	40.302
2	10	4.721	8.585	0.5499	44.861
5	11	3.613	6.935	0.5210	49.582
6	12	0.473	1.060	0.4462	53.195
7	13	0.928	2.070	0.4483	53.668
8	14	2.784	5.725	0.4863	54.596
9	15	2.375	5.235	0.4537	57.380
10	16	2.640	5.480	0.4818	59.755
12	17	3.569	8.300	0.4300	62.395

^aThe catch is in units of 1000 lbs. of lobster. The effort is in units of 1000 traps.

Table 2

Comparison of population size estimates and 95% confidence intervals for the regression model, and several logistic models for the lobster data from Seber (1973)

	Regression Model $p = \gamma f$	Constant Model (H_0) $\lambda^a = \beta_0$	Linear Model (H_1) $\lambda = \beta_0 + \beta_1 f$	Quadratic Model (H_2) $\lambda = \beta_0 + \beta_1 f + \beta_2 f^2$
Population Size	120,500	98,671	128,321	122,905
95% Confidence Interval	77,000 327,000	97,267 100,075	124,875 131,767	119,841 125,969

^a $\lambda = \log_e \{p/(1-p)\}$

Table 3

Comparison of expected catch values for the regression model, the constant probability model, the linear logistic model, and the quadratic logistic model for the lobster data from Seber (1973)

i	Observed Catch	Expected Catch			Quadratic Logistic
		Regression	Constant	Linear Logistic	
1	6,995	7,553	6,205	7,740	7,339
2	5,851	6,526	5,815	6,348	6,544
3	3,221	2,732	5,449	2,539	2,499
4	6,345	6,159	5,107	6,114	6,139
5	3,035	3,441	4,785	3,053	3,364
6	6,271	5,728	4,485	5,805	5,669
7	5,567	5,233	4,203	5,289	5,263
8	3,017	3,201	3,938	2,897	3,223
9	4,559	4,223	3,691	4,132	4,386
10	4,721	4,805	3,458	5,205	4,715
11	3,613	3,639	3,241	3,540	3,794
12	473	528	3,037	1,041	634
13	928	1,024	2,846	1,260	969
14	2,784	2,792	2,667	2,581	2,866
15	2,375	2,487	2,499	2,259	2,473
16	2,640	2,463	2,342	2,296	2,512
17	3,569	3,569	2,195	3,865	3,575

Table 4

Catch, effort, and temperature data for a 1951 lobster population
at Tignish, Canada taken from Paloheimo (1963)

Period	Catch (n_i)	Effort (f_i) ^a	Temperature (t_i)
1	29,900	18.321	1.7
2	168,000	145.253	3.0
3	172,500	168.528	4.9
4	130,300	106.532	5.7
5	71,300	78.862	5.5
6	99,400	145.530	5.4
7	50,200	117.863	7.1
8	47,300	130.757	10.7
9	26,400	34.978	13.7

^aThe effort is measured in units of a thousand trap hauls.

Table 5

Catch, effort, and temperature data for a 1950-51 lobster population
at Port Maitland, Canada taken from Paloheimo (1963)

Period	Catch (n_i)	Effort (f_i) ^a	Temperature (t_i)
1	60,400	33.664	7.9
2	49,500	27.743	7.7
3	28,200	17.254	6.3
4	20,700	14.764	3.5
5	11,900	11.190	3.1
6	15,600	16.263	2.9
7	13,200	14.757	3.1
8	25,400	32.922	3.25 ^b
9	29,900	45.519	3.4
10	32,500	43.523	3.6
11	24,700	37.478	4.0
12	27,600	43.367	5.9
13	22,200	37.960	6.1

^aEffort is in thousands of trap hauls.

^bThis value was missing, we used the average of the two adjoining periods.

Table 6

Comparison of parameter estimates (standard errors) for three models
for the Tignish lobster population of Paloheimo (1963)

Effort and Temperature Model (H_2)

<u>N</u>	<u>β_0</u>	<u>β_1</u>	<u>β_2</u>
807,519 (232)	-3.52 (0.0056)	0.0088 (0.000034)	0.28 (0.0012)

Effort Model (H_1)

<u>N</u>	<u>β_0</u>	<u>β_1</u>
1,222,734 (2828)	-3.31 (0.0057)	0.011 (0.000028)

Constant Probability Model (H_0)

<u>N</u>	<u>β_0</u>
1,174,986 (2386)	-2.01 (0.0038)

Table 7

Comparison of parameter estimates (standard errors) for three models
for the Port Maitland lobster population of Paloheimo (1963)

<u>N</u>	<u>β_0</u>	<u>β_1</u>	<u>β_2</u>
549,974 (2,389)	-3.94 (0.0091)	0.030 (0.00020)	0.11 (0.0010)

<u>Effort Model (H_1)</u>		
<u>N</u>	<u>β_0</u>	<u>β_1</u>
472,270 (1,092)	-3.29 (0.0054)	0.037 (0.00018)

<u>Constant Probability Model (H_0)</u>	
<u>N</u>	<u>β_0</u>
716,860 (4,210)	-2.89 (0.0086)

Table 8

Comparison of expected catch values for three models for
the Tignish lobster population of Paloheimo (1963)

Period	Observed Catch	Constant H_0	Expected Catch	
			Effort Only H_1	Effort + Temperature H_2
1	29,900	138,602	51,866	42,690
2	168,000	122,252	170,387	151,034
3	172,500	107,831	179,072	208,025
4	130,300	95,112	83,350	109,628
5	71,300	83,892	57,320	63,725
6	99,400	73,996	99,311	75,458
7	50,200	65,268	65,684	59,099
8	47,300	57,569	65,716	63,420
9	26,400	50,778	22,594	22,220

Table 9

Comparison of expected catch values for three models for the 1950-51
lobster population at Port Maitland, Canada of Paloheimo (1963)

Period	Observed Catch	Constant H_0	Expected Catch Effort Only H_1	Effort + Temperature H_2
1	60,400	37,715	53,986	63,120
2	49,500	35,731	39,287	46,641
3	28,200	33,851	24,895	27,263
4	20,700	32,070	21,335	17,600
5	11,900	30,383	17,697	14,679
6	15,600	28,784	19,998	16,044
7	13,200	27,270	17,774	15,023
8	25,400	25,835	30,935	24,644
9	29,900	24,476	41,090	32,998
10	32,500	23,188	32,181	28,635
11	24,700	21,968	22,399	22,755
12	27,600	20,812	23,509	29,448
13	22,200	19,717	16,715	22,788