ESTIMATION OF INSTANTANEOUS LAMPREY ATTACK RATE.
(BASED ON A MARKOV MODEL OF LAMPREY PREDATION WITH NON-STATIONARY ATTACK RATES AND SURVIVAL RATES.)

BU-276-M D. S. Robson April, 1970

Abstract

Throughout the lifetime of an individual fish, lamprey attacks are assumed to satisfy the conditions of a Poisson process with attack rate $\lambda(t)$ and conditional probability $s(t)$ of surviving an attack. This implies, for example, that if a fish is captured, tagged and released at age t_0 then the number of additional lamprey scars born by that fish when it is recaptured at age t_1 is a Poisson random variable with a mean value given by the integral of $s(t)\lambda(t)$ over the interval (t_0,t_1). The assumption that all fish of a given stock and year class are independently subject to the same Poisson process can be tested from batch releases and recaptures, and if this type of sampling continues throughout the lifespan of the year class then the integral of $s(t)\lambda(t)$ can be estimated piece-wise from the age of recruitment into the lamprey fishery to the limiting age of the year class.

In the combined catch records of a year class through its entire lifespan the frequency distribution of scars per fish is geometric if all mortality rates (fishing, natural, lamprey predation) stand in a proportional relationship. Slight departures from the geometric occur if either man or lampreys begin exploiting the stock first, but maintain proportional exploitation rates once both predators are in operation.

The incidence of fresh wounds in the catch reflects the current rate of lamprey attack, and this rate is estimable from the incidence of fresh wounds if the average duration of lamprey attachment is known for the given fish age and the given season.

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For a number of years and in a number of fisheries, records have been kept of the number of fish in the catch bearing evidence of having suffered lamprey attack. Such evidence ranges from presence of lamprey attached to the fish on capture, or fish with fresh and bleeding wounds, through fish with older, healing wounds and with scars from much earlier encounters. The relative frequency of freshly wounded fish in the catch clearly reflects the level intensity of lamprey predation at that time, and we consider here the explicit question of how to utilize these data to estimate the instantaneous lamprey attack rate.

This instantaneous attack rate may be defined with respect to a randomly chosen fish from any specified cohort as

$$\lambda(t) = \lim_{\Delta t \to 0} \frac{1-P\{\text{not attacked in } (t,t+\Delta t)\}}{\Delta t} \tag{1}$$

on the condition that the fish does not die from other causes during this short interval. Because some fish do survive lamprey attackes, as evidenced by the presence of scars, we shall suppose that $\lambda(t)$ has two components corresponding to fatal and non-fatal attacks,

$$\lambda(t) = [1-s(t)]\lambda(t) + s(t)\lambda(t) \quad , \tag{2}$$

and assume that a non-fatal attack at time t in no way influences a fish's chances for survival or his chances for further lamprey attacks. These assumptions together with the definitions (1) and (2) will be referred to as the non-stationary Morkov model.

Lamprey feeding following its attachment to a fish may continue for a period ranging from several hours to several days or even weeks, depending largely on the size of the lamprey. The cumulative frequency distribution $F_t(y)$ of feeding time y (= duration of lamprey attachment) thus depends upon the season of the year, and we shall suppose that the regression of feeding time on seasonal time, $\mu_t = E(y|t)$, is known from laboratory studies. With this information available it follows that from the catch made at time t the statistic

$$\ell(t) = \frac{\#(\text{one fresh wound, no scars})}{\#(\text{no wounds, no scars})}$$

estimates the function

$$\int_0^t \lambda(t-x)[1-F_{t-x}(x)]dx \approx \lambda(t)\mu_t$$

or

$$\hat{\lambda}(t) = \frac{\ell(t)}{\hat{\mu}_t} \quad .$$

For fish which survive to age t (and any fish captured at age t certainly survives to age t) the conditional probability of escaping completely from lampreys during this period is

$$\Pr\{\text{no wounds, no scars at age } t|\text{survive to age } t\} = e^{-\int_0^t s(x)\lambda(x)dx} \quad .$$

The conditional probability that a fish surviving to age t will be undergoing its first lamprey attack at time t is:

$$e^{-\int_0^t s(t)\lambda(x)dx} \int_0^t \lambda(t-x)[1-F_{t-x}(x)]dx$$

and hence the ratio of these two probabilities, estimated by $\ell(t)$, is an estimate of the integral:

$$\int_0^t \lambda(t-x)[1-F_{t-x}(x)]dx \quad .$$

In the spring when lampreys are small and feeding time is long the attack rate $\lambda(t)$ is a slowly changing function of t, as is $F_t(x)$; in August and early fall when the lamprey are maturing the feeding time is short and the attack rate is changing at a more rapid rate. This combination of circumstances supports the approximation

$$\lambda(t)\mu_t \approx \int_0^t \lambda(t-x)[1-F_{t-x}(x)]dx \quad .$$

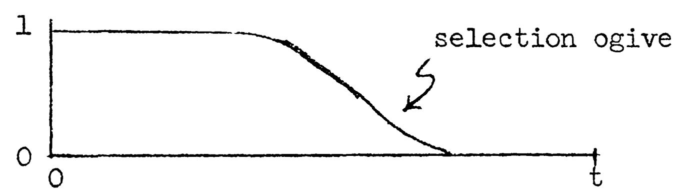
The estimator $\hat{\lambda}(t) = \ell(t)/\hat{\mu}_t$ is based only on fish having no scars, and sample size will therefore be relatively small in a population heavily preyed upon by lampreys. Intuitively, it would seem that fish bearing very old scars along with a fresh lamprey wound should be just as informative concerning the current incidence of lamprey attacks as fish bearing no scars whatsoever and a fresh lamprey wound. On the other hand, it is also intuitively clear that fish bearing a recent wound plus a fresh wound are under more severe stress than fish with just a recent wound, and that the ratio of these two frequencies would therefore lead to an underestimate of the attack rate. Thus, it would appear that we could increase our sample size by including scarred fish so long as we do not include fish with recent wounds.

Formalizing this reasoning, if ew first assume a sharp precision in identifying "old scars", so that a fish bearing a scar less than c units old is not included in the sample count, we find

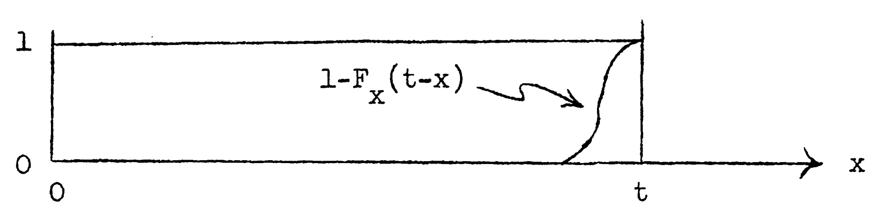
$$\frac{P(\text{caught at age t with a fresh wound and no other wounds less than c units old})}{P(\text{caught at age t with no wounds less than c units old})}$$

$$= \int_0^t \lambda(t-x)[1-F_{t-x}(x)]dx \doteq \lambda(t)\mu_t \quad .$$

In deriving this expression we assume that all stress caused by lamprey attacks prior to t-c has vanished so that the function $F_{t-x}(x)$ derived for healthy fish does apply ($x \ll c$). Insofar as this assumption is correct, the ratio indicated above is independent of c, and this invariance property holds true also if we replace the "knife-edge" selection at c by a selection ogive so long as the ogive:



drops to zero soon enough to exclude fish still under stress at the point where $1-F_x(t-x)$ begins its ascent:



(Note that I have here switched from $F_{t-x}(x)$ to $F_x(t-x)$ so that x is now the time at which the lamprey attack occurs, rather than at t-x; this should at once clarify and confuse matters.)

This invariance property allows us considerable freedom in deciding which fish to exclude from our counts, and relieves us of the necessity of tightly specifying our selection rule or its operating characteristics (ogive), so long as the investigator is consistent in selecting only those fish which had recovered from earlier attacks at the earliest time that a "freshly wounded" fish could have been attacked.

We thus arrive at the estimator

$$\hat{\lambda}(t) = \frac{1}{\hat{\mu}_t} \cdot \frac{\#(\text{caught at age t with a fresh wound but no other recent wounds})}{\#(\text{caught at age t with \underline{no} recent wounds})}$$

The Poisson model

$$P(x \text{ additional scars during } (t_0,t_1) | \text{alive at } t_1) = \frac{1}{x!}\left[\int_{t_0}^{t_1} s(t)\lambda(t)dt\right]^x e^{-\int_{t_0}^{t_1} s(t)\lambda(t)dt}$$

may be applied to tagged fish released at t_0 and recaptured at t_1. The tagged fish recaptured at t_1 form a cohort whose history of (non-fatal) lamprey attacks is known for the period (t_0,t_1). Applying this same model to the cohort consisting of fish of a given year class captured at time t and observed for scars we have

$$P(x \text{ scars} \mid \text{caught at age } t) = \frac{1}{x!}\left[\int_0^t s(y)\lambda(y)dy\right]^x e^{-\int_0^t s(y)\lambda(y)dy} .$$

Now the probability of death from fishing is

$$P(\text{caught}) = \int_0^\infty f(t)\, e^{-[M(t)+F(t)+\Lambda(t)-A(t)]}\, dt$$

where

$M(t) = \int_0^t m(y)dy$ is the integrated natural mortality rate

$F(t) = \int_0^t f(y)dy$ is the integrated (instantaneous) fishing mortality rate

$\Lambda(t) - A(t) = \int_0^t [\lambda(y)-s(y)\lambda(y)]dy$ is the integrated (instantaneous rate of fatal lamprey attacks

and the density function for "age at capture" of fish which are caught is therefore

$$g(t) = \frac{f(t)\, e^{-[M(t)+F(t)+\Lambda(t)-A(t)]}}{\int_0^t f(y)\, e^{-[M(y)+F(y)+\Lambda(y)-A(y)]}\, dy} .$$

The frequency distribution of number of lamprey scars per fish in the total, lifetime catch from this year class is therefore

$$P(x \text{ scars}|\text{caught}) = \int_0^\infty g(t)P(x \text{ scars}|\text{caught at } t)dt$$

$$= \frac{\int_0^\infty f(t) \frac{[A(t)]^x}{x!} e^{-[M(t)+F(t)+\Lambda(t)]} dt}{\int_0^\infty f(t) e^{-[M(t)+F(t)+\Lambda(t)-A(t)]} dt} .$$

In the special case where all rates are constant this reduces to

$$P(x \text{ scars}|\text{caught}) = \left(\frac{s\lambda}{m+f+\lambda} \right)^x \left(1 - \frac{s\lambda}{m+f+\lambda} \right)$$

which, in this steady state, would also be the frequency distribution of x in the catch of fish of all ages made at any one point in time.

More generally it may be noted that the geometric distribution obtains if all intensity functions are proportional to a common function:

$$f(t) = fg(t)$$

$$m(t) = mg(t)$$

$$\lambda(t) = \lambda g(t)$$

$$a(t) = \lambda sg(t) .$$

More specifically, if man and lamprey both start preying on the cohort at the same time in the life cycle of the fish then proportional intensity functions from that point onward would result in a geometric distribution of scar number in the lifetime catch from that year class. If lampreys start preying on the year class before they attain legal size, but at legal size all intensity functions become proportional then

$$P(x \text{ scars}|\text{caught}) = p^x(1-p)\, e^{-A_0} \left[1 + \frac{A_0}{p} + \frac{1}{2!}\left(\frac{A_0}{p}\right)^2 + \cdots + \frac{1}{x!}\left(\frac{A_0}{p}\right)^x\right]$$

where

$$p = \frac{s\lambda}{m+f+\lambda}$$

$$A_0 = \int_0^{t_r} s(t)\lambda(t)dt = A(t_r)$$

and t_r is the age of recruitment into the fishery. If A_0 is small, as expected, then

$$P(x \text{ scars}|\text{caught}) \doteq p^x(1-p)\, e^{+\frac{A_0}{p}(1-p)}$$

and even if A_0 is not small this approximation must still hold for large x. The mean and variance of this (exact) distribution are

$$\mu_x = A_0 + \frac{p}{1-p}$$

$$\sigma_x^2 = \mu_x + \left(\frac{p}{1-p}\right)^2$$

so that moment estimators of A_0 and p are

$$\hat{A}_0 = \bar{x} - \sqrt{s^2-\bar{x}} \qquad \hat{p} = \frac{\sqrt{s^2-\bar{x}}}{1+\sqrt{s^2-\bar{x}}} = \frac{\bar{x}-\hat{A}_0}{\bar{x}-\hat{A}_0+1}$$

This distribution, which could apply only if lampreys begin exploiting the fish before they reach legal size, has a concave shape on the log P scale and hence does not conform to a number of observed frequency distributions for lamprey scars. If we change our assumption to say that man begins exploiting a year class before the lamprey does then log $P(x)$ does become linear for $x > 0$ (again assuming proportional intensity functions starting at the time (age) of recruitment into the lamprey fishery). In this case we find

$$P(x \text{ scars} | \text{caught}) = \begin{cases} \dfrac{q+\theta}{1+\theta} & \text{for} \quad x = 0 \\ \\ \dfrac{p^x q}{1+\theta} & \text{for} \quad x > 0 \end{cases}$$

with p and q=1-p defined as before and

$$\theta = (m+f+\lambda-\lambda s)\, e^{[M(t_\ell)+F(t_\ell)]} \int_0^{t_\ell} f(t)\, e^{-[M(t)+F(t)]}\, dt$$

where t_ℓ is the age of recruitment into the lamprey fishery. The mean and variance of this distribution are

$$\mu_x = \frac{p}{q} \left(\frac{1}{1+\theta} \right)$$

$$\sigma_x^2 = \frac{p}{q^2} \left(\frac{1+\theta(1+p)}{1+\theta} \right)$$

and the maximum likelihood estimators of p and θ are

$$\hat{p} = 1 - \frac{1-r_0}{\bar{x}} \qquad \hat{\theta} = \frac{\hat{p}}{1-r_0} - 1$$

where $\bar{x}$ is the average number of scars per fish and r_0 is the proportion of fish with no scars. This proportion of zeroes should exceed $\hat{q}$; i.e., $r_0 > (1-r_0)/\bar{x}$, and when the data are plotted on the log scale and the line

$$\log \hat{P}(x) = x \log \hat{p} + \log \hat{q} - \log(1+\hat{\theta})$$

is drawn then log r_0 should fall above this line. A statistical test of this positive deviation is given by a one-tailed test of the 2x2 table:

			Total
	n_0	$n - n_0 - 1$	$n - 1$
	$n - n_0$	$\Sigma x - (n-n_0)$	Σx
Total	n	$\Sigma x - 1$	$n - 1 + \Sigma x$

where n is the sample size, Σx is the total number of scars observed in the sample and n_0 is the number of fish with no scars that occur in the sample. Only excessively large values of n_0 are to be judged statistically significant in this one-tailed test.

With lake trout data we might expect the earlier model to fit -- i.e. where lampreys start exploiting a year class before man does -- and then this same test would be applicable but small n_0 would be required for significance.
(* For a derivation of this result see the appendix.)

Let t_0 denote the time of release of a tagged fish and at a later time t let

$$P(\text{a non-fatal lamprey attack during } (t, t+\Delta t) \mid \text{alive at } t)$$

$$= s(t)\lambda(t)\Delta t + o(\Delta t)$$

$$P(\text{a fatal lamprey attack during } (t, t+\Delta t) \mid \text{alive at } t)$$

$$= [1 - s(t)]\,\lambda(t)\Delta t + o(\Delta t)$$

$$P(\text{death from other causes during } (t, t+\Delta t) \mid \text{alive at } t)$$

$$= p(t)\Delta t + o(\Delta t)$$

Under the conditions of a Poisson model we then have

$$P(x \text{ additional scars during } (t_0, t_1) \mid \text{alive at } t_1)$$

$$= \frac{1}{x!}\left[\int_{t_0}^{t_1} s(t)\lambda(t)dt\right]^x e^{-\int_{t_0}^{t_1} s(t)\lambda(t)dt}$$

where

$$P(\text{alive at } t_1 \mid \text{alive at } t_0) = e^{-\int_{t_0}^{t_1} [p(t) + \lambda(t) - s(t)\lambda(t)]dt}$$

Since $s(t)$ and $\lambda(t)$ are inseparable in this context we write $a(t) = s(t)\lambda(t)$ and $A(t) = \int a(t)dt$, so that

$$P(x \text{ additional scars during } (t_0,t_1) | \text{alive at } t_1)$$

$$= \frac{1}{x!} \left[A(t_1) - A(t_0)\right]^x e^{-[A(t_1) - A(t_0)]}$$

If n of the fish released at t_0 are recaptured at t_1 then the sum $S = \sum_1^n X_i$ is a sufficient statistic with

$$P(s|t_0,t_1) = \frac{n^s}{s!} \left[A(t_1) - A(t_0)\right]^s e^{-n[A(t_1) - A(t_0)]}$$

and if data are available from a number of releases and recaptures then the likelihood function is e^L where

$$L = \sum_{i,j} s_{ij} \log \left[A(t_j) - A(t_i)\right] - \sum_{i,j} n_{ij} \left[A(t_j) - A(t_i)\right]$$

$$+ \sum_{i,j} \log \frac{n_{ij}^{s_{ij}}}{s_{ij}!}$$

In the tagging example provided by Regier the likelihood is a function of 4 unknown parameters which may be defined as

$$\theta_1 = A(\text{June, } 67) - A(\text{June, } 66)$$
$$\theta_2 = A(\text{June, } 67) - A(\text{May, } 67)$$
$$\theta_3 = A(\text{July, } 67) - A(\text{June, } 67)$$
$$\theta_4 = A(\text{July, } 66) - A(\text{June, } 66)$$

The Poisson parameters for his 6 samples are then:

Release month	Recapture month	n_{ij}	s_{ij}	$A(t_j) - A(t_i)$
June 66	May 67	17	1	$\theta_1 - \theta_2$
"	June 67	45	5	θ_1
"	July 67	30	6	$\theta_1 + \theta_3$
July 66	May 67	44	1	$\theta_1 - \theta_2 - \theta_4$
"	June 67	64	4	$\theta_1 - \theta_4$
"	July 67	27	2	$\theta_1 + \theta_3 - \theta_4$

The log-likelihood function for these data is

$$L = -227\,\theta_1 + 61\,\theta_2 - 57\,\theta_3 + 135\,\theta_4 + \log(\theta_1 - \theta_2)$$
$$+ 5\log\theta_1 + 6\log(\theta_1 + \theta_3) + \log(\theta_1 - \theta_2 - \theta_4) + 4\log(\theta_1 - \theta_4)$$
$$+ 2\log(\theta_1 + \theta_3 - \theta_4)$$

and the likelihood equations are

$$\frac{\partial L}{\partial \theta_1} = -227 + \frac{1}{\theta_1 - \theta_2} + \frac{5}{\theta_1} + \frac{6}{\theta_1 + \theta_3} + \frac{1}{\theta_1 - \theta_2 - \theta_4} + \frac{4}{\theta_1 - \theta_4} + \frac{2}{\theta_1 + \theta_3 - \theta_4} = 0$$

$$\frac{\partial L}{\partial \theta_2} = 61 - \frac{1}{\theta_1 - \theta_2} - \frac{1}{\theta_1 - \theta_2 - \theta_4} = 0$$

$$\frac{\partial L}{\partial \theta_3} = -57 + \frac{6}{\theta_1 + \theta_3} + \frac{2}{\theta_1 + \theta_3 - \theta_4} = 0$$

$$\frac{\partial L}{\partial \theta_4} = 135 - \frac{1}{\theta_1 - \theta_2 - \theta_4} - \frac{4}{\theta_1 - \theta_4} - \frac{2}{\theta_1 + \theta_3 - \theta_4} = 0$$

These equations may be solved by a standard iterative procedure, beginning with initial values determined by an unweighted least squares analysis of the sample means. In the matrix notation for linear models, $Y = X\theta + \epsilon$, let

$$Y = \begin{bmatrix} \frac{1}{17} = .0588 \\ \frac{5}{45} = .1111 \\ \frac{6}{30} = .2000 \\ \frac{1}{44} = .0227 \\ \frac{4}{64} = .0625 \\ \frac{2}{27} = .0741 \end{bmatrix} \quad X = \begin{bmatrix} 1 & -1 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 \\ 1 & -1 & 0 & -1 \\ 1 & 0 & 0 & -1 \\ 1 & 0 & 1 & -1 \end{bmatrix} \quad \theta = \begin{bmatrix} \theta_1 \\ \theta_2 \\ \theta_3 \\ \theta_4 \end{bmatrix}$$

then

$$X'Y = \begin{bmatrix} .5292 \\ -.0815 \\ .2741 \\ -.1593 \end{bmatrix} \quad X'X = \begin{bmatrix} 6 & -2 & 2 & -3 \\ -2 & 2 & 0 & 1 \\ 2 & 0 & 2 & -1 \\ -3 & 1 & -1 & 3 \end{bmatrix} \quad (X'X)^{-1} = \begin{bmatrix} \frac{2}{3} & \frac{1}{2} & -\frac{1}{2} & \frac{1}{3} \\ \frac{1}{2} & 1 & -\frac{1}{2} & 0 \\ -\frac{1}{2} & -\frac{1}{2} & 1 & 0 \\ \frac{1}{3} & 0 & 0 & \frac{2}{3} \end{bmatrix}$$

and

$$\hat{\theta} = (X'X)^{-1}X'Y = \begin{bmatrix} .12190 \\ .04605 \\ .05025 \\ .07020 \end{bmatrix}$$

(Since regression estimates are more robust than maximum likelihood, one might be content to stop with these.) The predicted values from the regression equation are then

$$\hat{Y} = X\hat{\theta} = \begin{bmatrix} .07585 \\ .12190 \\ .17215 \\ .00565 \\ .05170 \\ .10195 \end{bmatrix}$$

and residual mean square

$$\tfrac{1}{2}(Y - \hat{Y})'(Y - \hat{Y}) = .001183$$

A somewhat simpler hypothesis would be that the function a(t) is periodic, repeating itself each year, and in the present example this would imply that $\theta_3 = \theta_4$. The difference $\hat{\theta}_3 - \hat{\theta}_4$ is clearly not statistically significant here, but the power of this test is extremely poor with only 2 degrees of freedom for error (part of the price paid for robustness). Under the hypothesis $\theta_3 = \theta_4$ we have

$$X = \begin{bmatrix} 1 & -1 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 1 \\ 1 & -1 & -1 \\ 1 & 0 & -1 \\ 1 & 0 & 0 \end{bmatrix} \quad \hat{\theta} = \begin{bmatrix} .1119 \\ .0400 \\ .0622 \end{bmatrix} \quad X\hat{\theta} = \begin{bmatrix} .0719 \\ .1119 \\ .1741 \\ .0097 \\ .0497 \\ .1119 \end{bmatrix}$$

and a residual sum of squares of .002605 with 3 degrees of freedom.

The preceding results may be interpreted to say that among fish surviving a given year the average number of lamprey attacks is .1119 (per fish); 35.7% of these attacks occur between (roughly) the middle of May and the middle of June, 55.6% between the middle of June and the middle of July, and 8.7% occur during the remainder of the year. (The roughness is due to rounding dates off to the nearest month.) The standard errors attaching to these figures, however, are quite large.

There is some indication that the data are less variable than the Poisson model would imply. We note that the residual sum of squares .002605 is an estimate of

$$E \sum_i (\hat{Y}_i - Y_i)^2 = \sum_i \operatorname{var}(Y_i) \sum_j c_{ij}^2$$

where C is the matrix

$$C = X(X'X)^{-1}X' - I = \begin{bmatrix} .40 & 0 & .20 & .40 & -.20 & 0 \\ 0 & -.75 & .25 & 0 & .25 & .25 \\ .20 & .25 & -.35 & -.20 & -.15 & .25 \\ .40 & 0 & -.20 & -.40 & .20 & 0 \\ -.20 & .25 & -.15 & .20 & -.35 & .25 \\ 0 & .25 & .25 & 0 & .25 & -.75 \end{bmatrix}$$

In the present case Y_i is a mean, $Y_i = s_i/n_i$, and under the Poisson model

$$\operatorname{var}(Y_i) = \frac{1}{n_i} E(Y_i)$$

hence, under this model,

$$E \sum_i (\hat{Y}_i - Y_i)^2 = E \sum_i \frac{Y_i}{n_i} \sum_j c_{ij}^2$$

For our data we find

$$\sum_i \frac{Y_i}{n_i} \sum_j c_{ij}^2 = .008175$$

and the (approximate) chi-square statistic on 3 degrees of freedom

$$\frac{.002605}{.008175} = .319$$

is significantly small (at the 5% level for a one-tailed test or the 10% level for a two-tailed test). This supports my own a priori suspicion regarding the temporal independence assumption in the Poisson model, and I accept the inference from the one-tailed test.

With regard to estimation methods, the conclusion to be drawn from the above significance test is that the optimal method is some weighted least squares analysis with weights which are not as variable as the Poisson model would imply, and until substantially more data are available I would be content with equal weighting. The question of optimal weighting is not of serious concern until data are available in which the interval at large for tagged fish is highly variable.

Appendix

Under the null hypothesis that $\theta = 0$ we have

$$P(x \text{ scars} | \text{caught}) = p^x q \quad \text{for} \quad x=0,1,2,\cdots$$

and the probability that in a sample of (given) size n we will observe n_0 fish with no scars is

$$P_n(n_0) = \binom{n}{n_0} q^{n_0} p^{n-n_0} \quad .$$

Given that a fish has at least one scar, the probability that it has x scars is

$$P(x \text{ scars} | x \geq 1) = \frac{p^x q}{1-q} = p^{x-1} q$$

and the sum of $n-n_0$ such (independent and identically distributed) random variables is then distributed as

$$P_n\left(\sum_1^{n-n_0} x_i = T | x_1, \cdots, x_{n-n_0} \geq 1 \right) = \binom{T-1}{n-n_0-1} p^{T-(n-n_0)} q^{n-n_0} \quad .$$

The joint probability distribution of n_0 and $\sum_1^{n-n_0} x_i$, for fixed n, is therefore

$$P_n\left(n_0, \sum_1^{n-n_0} x_i = T\right) = \binom{n}{n_0}\binom{T-1}{n-n_0-1} p^T q^n$$

and since the marginal distribution of $\sum_1^{n-n_0} x_i = T$ is

$$P_n\left(\sum_{i=1}^{n-n_o} x_i = T\right) = \binom{n+T-1}{T} p^T q^n$$

then

$$P_n(n_o|T) = \binom{n}{n_o}\binom{T-1}{n-n_o-1}\Big/\binom{n+T-1}{T} .$$