How Extreme Events Can Affect a Seemingly Stabilized Population: a Stochastic Rendition of Ricker's Model

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Abstract

Our paper computationally explores Ricker's *predator satiation* model with the objective of studying how the extinction dynamics of an animal species having a two-stage life-cycle is affected by a sudden spike in mortality due to an extraneous extreme event. Our simulation model has been designed and implemented using sockeye salmon population data based on a stochastic version of Ricker's model; with the shock size being reflected by a sudden reduction in the carrying capacity of the environment for this species. Our results show that even for a relatively marginal increase in the negative impact of an extreme event on the carrying capacity of the environment, a species with an otherwise stable population may be driven close to extinction.

Key words: Ricker's model, extinction dynamics, extreme event, Monte Carlo simulation

Background and research objective

PVA approaches do not normally consider the risk of catastrophic extreme events under the pretext that no population size can be large enough to guarantee survival of a species in the event of a large-scale natural catastrophe. [1] Nevertheless, it is only very intuitive that some species are more "delicate" than others; and although not presently under any clearly observed threat, could become threatened with extinction very quickly if an *extreme event* was to occur even on a low-to-moderate scale. The term "extreme event" is preferred to "catastrophe" because catastrophe usually implies a natural event whereas; quite clearly; the chance of man-caused extreme events poses a much greater threat at present to a number of animal species as compared to any large-scale natural catastrophe.

An animal has a two-stage life cycle when; in the first stage, newborns become immature youths and in the second stage; the immature youths become mature adults. Therefore, in terms of the stage-specific approach, if Y_t denotes the number of immature young in stage t and A_t denotes the number of mature adults, then the number of adults in year t + 1 will be some proportion of the young, specifically those that survive to the next (reproductive) stage. Then the formal relationship between the number of mature adults in the next stage and the number of immature youths at present may be written as follows:

$$A_{t+1} = \lambda Y_t$$

Here λ is the survival probability, i.e. it is the probability of survival of a youth to maturity. The number of young next year will depend on the number of adults in t:

$$Y_{t+1} = f(A_t)$$

Here f describes the reproduction relation between mature adults and next year's young.

This is a straightforward system of simultaneous difference equations which may be analytically solved using a variation of the *cobwebbing approach*. [2] The solution process begins with an initial point (Y_1, A_1) and iteratively determines the next point (Y_2, A_2). If *predator satiation* is built into the process, then we simply end up with Ricker's model:

$$Y_{t+1} = \alpha A_t e^{-At/K}$$

Here α is the maximum reproduction rate (for an initial small population) and K is the population size at which the reproduction rate is approximately half its maximum [3]. Putting $\beta = {}^1/_K$ we can re-write Ricker's equation as follows:

$$Y_{t+1} = \alpha A_t e^{-\beta At}$$

It has been shown that if (Y_0, A_0) lies within the first of three possible ranges, (Y_n, A_n) approaches (0, 0) in successive years and the population becomes extinct. If (Y_0, A_0) lies within the third range then (Y_n, A_n) equilibrate to a steady-state value of (Y^*, A^*). Populations that begin with (Y_0, A_0) within the second range oscillate between $(Y^*, 0)$ and $(0, A^*)$. Such alternating behavior indicates one of the year classes, or cohorts, become extinct while the other persists i.e. adult breeding stock appear only every other year. Thus the model reveals that three quite different results occur depending initially only on the starting sizes of the population and its distribution among the two stages. [4]

We use the same basic model in our research but instead of analytically solving the system of difference equations, we use the same to simulate the population dynamics as a stochastic process implemented on an MS-Excel spreadsheet. Rather than using a closed-form equation like Ricker's model to represent the functional relationship between Y_{t+1} and A_t, we use a Monte Carlo method to simulate the stage-transition process within

Ricker's framework; introducing a massive perturbation with a very small probability in order to emulate a catastrophic event.[5]

Conceptual framework

We have a formulated a stochastic population growth model with an inbuilt capacity to generate an extreme event based on a theoretical probability distribution. The non-stochastic part of the model corresponds to Ricker's relationship between Y_{t+1} and A_t. The stochastic part has to do with whether or not an extreme event occurs at a particular time point. The gamma distribution has been chosen to make the probability distribution for the extreme event a skewed one as it is likely to be in reality. Instead of analytically solving the system of simultaneous difference equations iteratively in some variation of the cobwebbing method, we have used them in a spreadsheet model to simulate the population growth over a span of ten time periods.

We apply a computational methodology whereby the initial number of immature young is hypothesized to either attain the expected number predicted by Ricker's model or drastically fall below that number at the end of every stage, depending on whether an extraneous extreme event does not occur or actually occurs. The mortalities as a result of an extreme event at any time point is expressed as a percentage of the pristine population size for a clearer comparative view.

Model building

Among various faunal species, the population dynamics of the sockeye salmon (*oncorhynchus nerka*) has been most extensively studied using Rickert's model. Salmon are unique in that they breed in particular fresh water systems before they die. Their offspring migrates to the ocean and upon reproductive maturity, they are guided by a hitherto unaccounted instinctive drive to swim back to the very same fresh waters where they were born to spawn their own offspring and perish. Salmon populations thus are very sensitive to habitat changes and human activities that have a negative impact on riparian ecosystems that serve as breeding grounds for salmon can adversely affect the peculiar life-cycle of the salmon. Many of the ancient salmon runs (notably those in California river systems) have now gone extinct and it is our hypothesis that an even seemingly stabilized population can be rapidly driven to extinction due to the effect of an extraneous (quite possibly man-made) extreme event with the capacity to cause mass mortality. The following table shows the four-year averages of the sockeye salmon population in the Skeena river system in British Columbia in the first half of the twentieth century.

Year	Population (in thousands)
1908	1,098
1912	740
1916	714
1920	615
1924	706
1928	510
1932	278
1936	448
1940	528
1944	639
1948	523

(*Source*: *http://www-rohan.sdsu.edu/~jmahaffy/courses/s00/math121/lectures/product_rule/product.html#Ricker'sModel*)

A non-linear least squares best-fit to Ricker's model is obtained for the above set of data is obtained as follows:

Minimize $\varepsilon^2 = \sum_{t=1}^{n} [d_t - \{\alpha A_t e^{-\beta A_t}\}]^2$, where d_t is the actual population size in year t.

The necessary conditions to the above least squares best-fit problem is obtained as follows:

$\partial(\varepsilon^2)/\partial\alpha = \partial(\varepsilon^2)/\partial\beta = 0$; whereby we get $\alpha^* \approx 1.54$ and $\beta^* \approx 7.8 \times 10^{-4}$

Plugging these parameters into Ricker's model indeed yields a fairly good approximation of the salmon population stabilization in the Skeena river system in the first half of the previous century.

As the probability distribution of an extraneous extreme event is likely to be a highly skewed one, we have generated our random variables from the cumulative distribution function (*cdf*) of the gamma distribution rather than the normal distribution. The distribution boundaries are fixed by generating random integers in the range 1 to 100 and using these random integers to define the shape and scale parameters of the gamma distribution. The gamma distribution performs better than the normal distribution when the distribution to be matched is highly right-skewed; as is desired in our model. The combination of a large variance and a lower limit at zero makes fitting a normal distribution rather unsuitable in such cases.[6] The probability density function of the gamma distribution is given as follows:

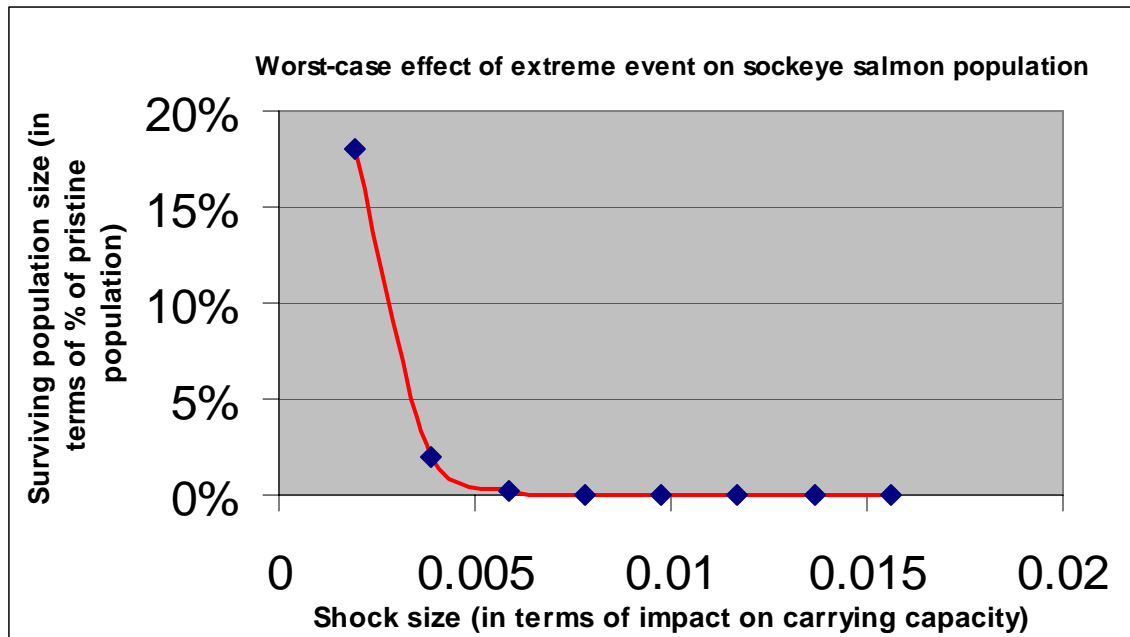$$f(x, a, b) = \{b^{a}\Gamma(a)\}^{-1}x^{a-1}e^{-x/b} \text{ for } x > 0$$

Here α > 0 is the shape parameter and β > 0 is the scale parameter of the gamma distribution. The cumulative distribution function may be expressed in terms of the *incomplete gamma function* as follows:

$$F(x, a, b) = \int_{0}^{x} f(u)du = \gamma(a, x/b)/\Gamma(a)$$

In our spreadsheet model, we have F (R, R/2, 2) as our *cdf* of the gamma distribution. Here R is an integer randomly sampled from the range 1 to 100. An interesting statistical result of having these values for x, α and β is that the cumulative gamma distribution value becomes equalized with the value $[1 - \chi^{2}(R)]$ having R degrees of freedom, thus allowing χ^{2} *goodness-of-fit* tests. [7]

Our model is specifically designed to simulate the extinction dynamics of sockeye salmon population using a stochastic version of Ricker's model; with the shock size being based on a sudden reduction in the parameter K i.e. the carrying capacity of the environment for this species. The model parameters are same as those of Ricker's model i.e. α and β (which is the reciprocal of K). We have kept α constant at all times at 1.54, which was the least squares best-fit value obtained for that parameter. We have kept a β of 0.00078 (i.e. the best-fit value) when no extreme event occurs and have varied the β between 0.00195 and 0.0156 (i.e. between 2.5 times to 20 times the best-fit value) for cases where an extreme event occurred. We have a third parameter *c* which is basically a 'switching constant' that determines whether an extreme event occurs or not. The switch is turned on triggering an extreme event when a random draw from a cumulative gamma distribution yields a value less than or equal to *c*. Using F (R, R/2, 2) as our *cdf* of the gamma distribution where R is a randomly drawn integer in the range (1, 100) means that the cumulative gamma function will randomly select from the approximate interval 0.518 ~ 0.683. By fixing the value of *c* at 0.5189 in our model we have effectively reduced the probability of occurrence of an extreme event to a miniscule magnitude relative to that of an extreme event not occurring. We have used the sockeye salmon population data from the table presented earlier For each level of the β parameter, we simulated the system and observed the maximum possible number of mortalities from an extreme event at that level of β. The results are reported below.

Results obtained from the simulation model

Worst-case effect of extreme event on sockeye salmon population

Surviving population size (in terms of % of pristine population) vs. *Shock size (in terms of impact on carrying capacity)*

We made 100 independent simulation runs for each of the eight levels of β. The low probability of extreme event assigned in our study yielded a mean of 1.375 for the number of observed worst-case scenarios (i.e. situations of maximum mortality) with a standard deviation of approximately 0.92. The worst-case scenarios for our choice of parameters necessarily occur if the extreme event occurs in the first time point when the species population is at its maximum size. Our model shows that in worst-case scenarios, the size of surviving population after an extreme event that could seed the ultimate recovery of the species to pre-catastrophe numbers (staying within the broad framework of Ricker's model) drops from about 18% of the pristine population size for a shock size corresponding to 2.5 times the best-fit β; to only about 0.000005% of the pristine population size for a shock size corresponding to 20 times the best-fit β.

Therefore, if the minimum required size of the surviving population is at least say 20% of the pristine population in order to survive and recover to pre-catastrophe numbers, the species could go extinct if an extreme event caused a little more than two-fold decrease in the environmental carrying capacity! Even if the minimum required size for recovery was relatively low at say around 2% of the pristine population, an extreme event that caused a five-fold decrease in the environmental carrying capacity could very easily force the species to the brink of extinction. An immediate course of future extension of our work would be allowing the fecundity parameter α to be affected by extreme events as is very likely in case of say a large-scale chemical contamination of an ecosystem due to a faulty industrial waste-treatment facility.

Conclusion

Our study has shown that even for a relatively marginal 2.5-fold decrease in the environmental carrying capacity due to an extreme event, a worst-case scenario could mean a mortality figure well above 80% of the pristine population. As a guide for future PVA studies we may suggest that one should not be deterred simply by the notion that extreme events are uncontrollable and hence outside the purview of computational modeling. Indeed the effect of an extreme event can almost always prove to be fatal for a species but nevertheless, as our study shows, there is ample scope and justification for future scientific enquiries into the relationship between survival probability of a species and the adverse impact of an extreme event on ecological sustainability.

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