

CORRESPONDENCE

From:

Atilio L. Coan
National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038, U.S.A.

Dr. Robert C. Francis
Inter-American Tropical Tuna Commission
c/o Scripps Institution of Oceanography
La Jolla, California 92037, U.S.A.

To The Editor of *Biometrics*:

On Jensen's Comparison of Logistic Equations for Population Growth

In a recent issue of this Journal, Jensen (1975) compared different logistic equations of population growth and applied a production model to data on brook trout. He arrived at several conclusions, which we believe are unwarranted and caused by errors of several types. These errors are discussed here in the order in which they occurred in Jensen's paper.

First, Jensen inappropriately used a derivation of equation (1), $\frac{dN}{dt} = rN \left(\frac{K-N}{K} \right)$, (Pielou 1969) to arrive at the conclusion that equation (2), $\frac{dN}{dt} = bN \left(\frac{K-N}{K} \right)$, is more realistic than equation (1) as it describes the birth and death processes more realistically. He did this by using and extending Pielou's derivation to show that the limit of the birth rate, $\lambda(N) = a_1 - b_1N$, and the death rate, $\mu(N) = a_2 + b_2N$, as the population reaches equilibrium is 0. This result was obtained because Jensen misinterpreted Pielou's analysis. Pielou stated in her proof that as "the population reaches equilibrium at the saturation level, the birth rate and the death rate are equal" (page 22). This statement does not exclude the possibility that both the birth and death rates are zero; however, Pielou omitted this condition by defining $a_1, a_2 > 0$ and $b_1, b_2 \geq 0$ for $\lambda(N)$ and $\mu(N)$. Therefore, since the death rate is always greater than zero, the birth and death rates could never be zero and equation (1) still gives a realistic biological outcome.

Second, Jensen was apparently unaware of Pielou's definition of $\lambda(N)$ and $\mu(N)$ as linear functions as he defined $\lambda(N)$ and $\mu(N)$ as nonlinear functions and showed that the growth equation will never be logistic. He stated that there are three cases in which an equilibrium between births and deaths can be approached: A) a constant instantaneous birth rate per individual and an instantaneous death rate per individual which approaches the birth rate as the carrying capacity is approached, B) a constant instantaneous death rate per individual and an instantaneous birth rate per individual which approaches the death rate as the carrying capacity is approached, and C) an instantaneous birth and death rate per individual which approaches a constant value as the carrying capacity is reached (Wrigley 1969). Jensen, by defining $\lambda(N)$ and $\mu(N)$ as linear functions, showed that Case A gives the logistic equation. Then by choosing two non-linear functions for $\lambda(N)$ and $\mu(N)$ in Cases B and C, he concluded that only in Case A will the growth equation of a population be logistic. This conclusion is not true. Pielou's derivation gives all three of these cases in her generalized equations for $\lambda(N)$ and $\mu(N)$ and, as long as $\lambda(N)$ and $\mu(N)$ are linear, the growth equation will always be logistic.

Finally, Jensen's application of the production model to data on brook trout (McFadden, Alexander and Shetter 1967) contained a number of errors. The data of McFadden *et al.* started with the 1949 cohort, which Jensen used and labeled erroneously as the 1947 cohort. He also stated that the instantaneous fishing mortality rate was estimated as $F = 0.35$ by McFadden *et al.* Actually McFadden *et al.* estimated an annual fishing mortality rate of 0.35 which is not the same as an instantaneous rate. Furthermore, Jensen used a group of equations utilizing data from the life table of an exploited population to estimate r , the intrinsic rate of population increase, which he then equated to the parameter k in the logistic surplus production model. His estimate of r was incorrect since it should have been derived from data generated by an unexploited population. As a result his estimate of the intrinsic rate of population increase was negative and his results from the production model analysis were unreasonable.

We have shown that errors in interpreting and extracting data from published sources as well as misinterpretations of analytical results led Jensen to unwarranted conclusions. We hope this letter accompanied by Jensen's response will provide a clearer understanding of the logistic growth equation.

References

- Jensen, A. L. (1975). Comparison of logistic equations for population growth. *Biometrics* 31, 853-962.
McFadden, J. T., Alexander, G. R. and Shetter, D. S. (1967). Numerical changes and population regulation in brook trout *Salvelinus fontinalis*. *J. Fish. Res. Bd. Canada* 24, 1425-1458.
Pielou, E. C. (1969). *An Introduction to Mathematical Ecology*. Wiley-Interscience, New York.
Wrigley, E. A. (1969). *Population and History*. McGraw-Hill, New York.

The author replied as follows:

I assumed that because $\lambda(N) = b - bN/K$ and $\mu(N) = d - dN/K$ gave $dN/dt = rN - dN^2/K$, that these were the birth and death rates per individual for equation (1). As stated by Coan and Francis this is not a valid argument because other expressions for $\lambda(N)$ and $\mu(N)$ also lead to the equation $dN/dt = rN - rN^2/K$. As a result, I do not succeed in showing that the birth rate and death rate in equation (1) approach zero as the carrying capacity is approached.

I still think the meaning of equation (1) is unclear. To derive equation (1) from equation (6) it must be assumed that $a_1 - a_2 = r$. My analysis shows that $a_1 - a_2$ is not the instantaneous rate of increase per individual as this would mean that the maximum sustainable yield of every fish population is zero. It often is assumed that $a_1 - a_2$ is the maximum instantaneous rate of increase per individual but in the logistic equation the instantaneous rate of increase per individual, dN/dt , has no maximum for $N > 0$. At best it can be said that $a_1 - a_2$ can be approximated by determination of r in an "uncrowded condition." The parameter $a_1 - a_2$ relates the instantaneous rate of change per individual, which is a function of population size, to the degree of saturation.

I did not realize that cases A, B and C could be described by equation (6). As a result of the equations I used for $\lambda(N)$ and $\mu(N)$ I incorrectly concluded logistic growth occurred only in case A. If equation (6) is applied, the growth equations for all three cases are logistic but all are of somewhat different form. Only the parameters of the equation $dN/dt = bN - bN^2/K$, which is obtained in case A if $a_2 = 0$, can be estimated directly from a life table. This appears to be the only case in which the parameters a_1 , a_2 , b_1 and b_2 can be identified directly in terms of r , b and d .

McFadden, Alexander and Shetter (1967) estimated the annual fishing mortality of ages 0-I as 23.6 percent and the annual fishing mortality of ages I-II as 35.1 percent. Fishing mortality for other age groups could not be determined but most fish caught by anglers were aged 0-II. I took the simple mean of 23.6 and 35.1 to obtain an annual mortality of 29.3 percent which gives an instantaneous mortality coefficient of about 0.35 as stated in my paper. If I use 35 percent as the annual mortality I obtain an instantaneous fishing mortality coefficient of 0.43 which is even closer to the optimum value of 0.47 calculated from the surplus production model based on the equation $dN/dt = bN - bN^2/K$.

The life table I used is the 1949 life table as stated by Coan and Francis and not the 1947 life table as I stated in my paper.

Exploitation is irrelevant as concerns estimation of r from a life table. Lotka showed that if the birth rate per individual and the death rate per individual are constant, the population growth equation converges to the equation $dN/dt = rN$ and he provided an equation for calculation of r . No statement is made concerning the sources of mortality (Keyfitz 1968). For the brook trout population the mortality and fecundity appear to have been constant for many years and the parameters of the equation $dN/dt = bN - bN^2/K$ can be calculated from a life table.

A. L. Jensen
School of Natural Resources
University of Michigan
Ann Arbor, Michigan 48109, U.S.A.

References

- Keyfitz, N. (1968). *Introduction to the Mathematics of Population*. Addison-Wesley, Reading, Massachusetts.
- McFadden, J. T., Alexander, G. R. and Shetter, D. S. (1967). Numerical changes and population regulation in brook trout *Salvelinus fontinalis*. *J. Fish. Res. Bd. Canada* 24, 1425-1458.