

# A Stochastic Age-Structured Population Model of Striped Bass (*Morone saxatilis*) in the Potomac River<sup>1</sup>

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COHEN, J. E., S. W. CHRISTENSEN, AND C. P. GOODYEAR. 1983. A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac River. *Can. J. Fish. Aquat. Sci.* 40: 2170–2183.

Deterministic age-structured models of fish populations neglect apparently stochastic fluctuations in the catch per unit effort of yearlings and of adult fish. We describe a model of an age-structured population in which the survival of eggs to yearlings fluctuates randomly, but all other age-specific rates of survival and of egg-laying are constant. For such a stochastic model, two measures of the long-term population growth rate are the average growth rate of the population size and the growth rate of the average population size. We compute both measures analytically for a simplified model representing only eggs and reproductive adults. For a model of the striped bass (*Morone saxatilis*) population spawning in the Potomac River, we compute both point and interval estimates of the growth rate of the average population size. We illustrate some statistical tests of the correctness of our stochastic model.

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Les modèles déterministes, structurés par âge, de populations de poissons négligent les fluctuations apparemment stochastiques des prises par unité d'effort de poissons de l'année et de poissons adultes. Nous décrivons dans l'article qui suit une population structurée par âge dans laquelle la survie des oeufs jusqu'à l'âge d'un an fluctue de façon aléatoire, alors que tous les autres taux particuliers à l'âge de survie et de déposition des oeufs sont constants. Dans un modèle stochastique de ce genre, le taux de croissance moyen de l'effectif de la population et le taux de croissance de l'effectif moyen de la population sont deux mesures de la croissance à long terme de cette population. Nous calculons les deux mesures analytiquement, dans un modèle simplifié représentant seulement les oeufs et les adultes reproducteurs. Dans le cas d'un modèle de population de bars rayés (*Morone saxatilis*) frayant dans le Potomac, nous produisons des estimations à la fois ponctuelles et par intervalles du taux de croissance de l'effectif moyen de la population. Nous donnons quelques exemples de tests statistiques de notre modèle stochastique.

Received February 23, 1983

Accepted August 11, 1983

Reçu le 23 février 1983

Accepté le 11 août 1983

To measure the actual and potential impact of power plant operations on fish populations, one must construct mathematical models of the fish populations. Deterministic age-structured models that employ the Leslie matrix (Keyfitz 1968) neglect apparently stochastic fluctuations in fish populations. Fisheries biologists have generalized the Leslie ma-

trix by incorporating stochastic fluctuations in one or more age-specific vital rates. The behavior of these models has been studied primarily by numerical computation (Allen and Basasibwaki 1974; Jensen 1975; Vaughan 1977a, 1977b; DeAngelis et al. 1977; Christensen et al. 1982; Deriso 1980; Ginzburg et al. 1983; D. Ludwig and C. J. Walters, unpublished data).

Independently of these developments among students of fish populations, students of mallard (*Anas platyrhynchos*) populations (Anderson 1975) and of human populations (LeBras 1974; Cohen 1976) investigated the effects on popu-

<sup>1</sup>Publication No. 2236, Environmental Sciences Division, Oak Ridge National Laboratory.

lation growth of random fluctuations in age-specific vital rates. Analytical approaches to computing long-run growth rates have been developed (Cohen 1977a, 1977b, 1979a, 1979b, 1979c, 1980; Lange 1979; Lange and Hargrove 1980; Lange and Holmes 1981; Tuljapurkar and Orzack 1980).

Our first purpose was to analyze a model developed by fisheries biologists, using the mathematical methods just cited, and then compute long-run growth rates of fish populations subject to random fluctuations in the survival of eggs. Our second purpose was to show how to approximate the sampling variability in the estimate of the long-run growth rate of average population size. Our third purpose was to illustrate statistical methods for testing whether the model is appropriate to real data of the rather limited, and less than scientifically ideal, kind that are likely to be available in practical situations in which many managerial and regulatory decisions are required.

We use data on the population of striped bass (*Morone saxatilis*) spawning in the Potomac River. We anticipate that these results will aid evaluations of the aquatic impact of power plants by making it possible to calculate long-run effects on growth rates of fish populations.

### Age-Structured Model with Random Survival of Eggs

We consider a female population of fish at yearly intervals just after the spawning of eggs in early spring. We take the unit of time to be 1 yr. We let  $t = 0$  be the time of initial observation,  $y_0(t)$  the number of the newly spawned female eggs at time  $t$ , and  $y_i(t)$  the number of  $i$ -yr-old female fish at the end of the spawning season in year  $t$ , where  $i = 1, 2, \dots, k$  and  $k$  is the maximum age of fish considered. We let  $y(t)$  be the column vector with elements  $y_0(t), y_1(t), \dots, y_k(t)$ . We shall call  $y(t)$  the age census at time  $t$ .

It is realistic to attribute the eggs spawned in year  $t$  to the female population alive in year  $t$ . Assuming no density dependence in the laying of eggs, we suppose, with  $F_i = 0$  for all nonreproductive age-classes, that

$$y_0(t) = \sum_{i=1}^k F_i y_i(t)$$

where  $F_i$  is the average number of female eggs laid in year  $t$  per female fish aged  $i$  in that year and  $F_k > 0$ . Define  $F_0 = 0$ , since eggs lay no eggs. The post-egg female population at time  $t$  (neglecting immigration) consists of the survivors of the female population (including eggs) at time  $t - 1$ :

$$y_i(t) = s_{i-1} y_{i-1}(t - 1), \quad i = 1, \dots, k$$

where  $s_i > 0$  is the fraction of female individuals (eggs or fish) aged  $i$  at  $t - 1$  who survive in the population (neither dying nor emigrating) to age  $i + 1$  at time  $t$ .

In conventional Leslie matrix models, this year's births (eggs) are usually attributed to last year's female population, rather than to this year's, as in the first equation above. To express  $y_0(t)$  in terms of the post-egg female population at time  $t - 1$ , we define  $s_k = 0, F_{k+1} = 1$  (we could pick any finite value for  $F_{k+1}$ ), and the effective fecundity of age

class  $i$  by

$$E_i = F_{i+1} s_i, \quad i = 0, \dots, k.$$

Then upon substitution, since  $E_k = 0$ ,

$$\begin{aligned} y_0(t) &= \sum_{i=1}^k F_i s_{i-1} y_{i-1}(t-1) + E_k y_k(t-1) \\ &= \sum_{j=0}^k E_j y_j(t-1). \end{aligned}$$

Thus, changes over time in the age census can be described in the conventional way by

$$(1) \quad y(t) = L(t)y(t-1)$$

where  $L(t)$  is a  $(k + 1) \times (k + 1)$  Leslie matrix:

$$(2) \quad L(t) = \begin{bmatrix} E_0 & E_1 & E_2 & \dots & E_{k-1} & E_k \\ s_0(t) & 0 & 0 & \dots & 0 & 0 \\ 0 & s_1 & 0 & \dots & 0 & 0 \\ 0 & 0 & s_2 & \dots & 0 & 0 \\ \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ 0 & 0 & 0 & \dots & s_{k-1} & 0 \end{bmatrix}$$

We assume in (2) that all elements of the Leslie matrix are constant over time except  $s_0(t)$ , the survival of eggs at time  $t - 1$  to age class 1 at time  $t$ . For  $E_0 = F_1 s_0(t)$  to be independent of  $t$ , we must have  $E_0 = F_1 = 0$ . The assumption that all elements of  $L(t)$  are constant except  $s_0(t)$  is a simplification as a first step in model building. Although we recognize that other elements of  $L(t)$  vary, we believe that the overwhelming source of variation lies in the survival of eggs (Hunter 1976). In particular, we assume that the variation in the survival of eggs is large compared even with the variation in adult mortality due to changes in fishing over time. If this last assumption is false, the effect on our results is outlined briefly below, at the end of the summary of our data analytic procedure and results, and in greater detail by C. P. Goodyear, J. E. Cohen, and S. W. Christensen (unpublished data). The present model and methods should not be used without modification in situations in which this assumption is known to be false.

This model is relevant to cases other than fish populations. Among white-crowned sparrows (*Zonotrichia leucophrys nuttali*) in coastal California, mortality varies mainly during the period from fledging to January 1 and not significantly thereafter (Baker et al. 1981, p. 643). If annual age classes were used for these birds, mortality variation would be concentrated in survival to age 1, as in the model (2).

As is standard in probability theory, we shall use the symbol  $E(\cdot)$  to denote the average, mean, or expected value of whatever random variable is enclosed in parentheses.

To complete the description of the model, we specify that the average survival  $E(s_0(t))$  of eggs is identical from year to year and that the survival in any one year is independent of the survival in any other year. Thus, the random variables  $s_0(t)$  are independent and  $E(s_0(t))$  is independent of  $t$ . These strong assumptions can be tested.

If the weather at the time of spawning is the principal influence on the survival of eggs (Ulanowicz and Polgar 1980), it may be reasonable to guess that the weather at that season is independent from year to year. However, analytical methods exist for analyzing models in which the distribution of Leslie matrix elements in one year does depend on the Leslie matrix elements that occurred the previous year. For the present model of independence from year to year, we shall be applying only a special case of those methods.

How should the long-run growth rate of a population with stochastic vital rates be measured? When the Leslie matrix is constant over time, so that  $L(t) = L$ , there is only one answer (Keyfitz 1968): the intrinsic rate of natural increase  $r$  of the population is the natural logarithm of the dominant eigenvalue of  $L$ . (Henceforth, we shall always use log and logarithm to mean natural logarithm.) Following is the reason for this choice when  $L(t) = L$ . For large times  $t$ , nonzero elements of  $L^t$  are proportional to the  $t$ th power of the dominant eigenvalue of  $L$ , which is the same as  $e^{rt}$ , and therefore so are all elements of the age census  $y(t)$ . If  $Y(t)$  is the total population size at time  $t$ , then for large values of  $t$ ,  $Y(t)$  is proportional to  $e^{rt}$ . Using  $c$  for the constant of proportionality, we have, when the Leslie matrix is constant,

$$(3) \quad Y(t)/e^{rt} = c \text{ for large } t.$$

Taking logarithms of both sides of (3), dividing by  $t$ , and letting  $t$  become large gives

$$(4) \quad r = \lim_{t \rightarrow \infty} (1/t) \log Y(t).$$

Since the asymptotic rate of growth is the same for all age classes in both the deterministic measure (4) and the stochastic measures (5) and (6), it makes no difference here whether nonreproductive age classes are included in  $Y(t)$  or excluded.

When  $L(t)$  varies randomly, so does  $Y(t)$ , and there is no unique "intrinsic rate of natural increase." Instead, there are several possible generalizations of (4). It becomes necessary to choose some overall measure of the behavior of  $\lim_{t \rightarrow \infty} (1/t) \log Y(t)$ . One possibility is to take the median of  $\lim_{t \rightarrow \infty} (1/t) \log Y(t)$  as a measure of population growth rate. Two other possibilities that have been studied analytically, and which we shall now describe in more detail, are to compute the average of the growth rate of population size and the growth rate of the average population size. It is important to realize that these two are different measures of population growth rate. Both measures of population growth rate have been studied in the context of fishing yield by Vaughan (1977a).

The average of the growth rate of population size is, by definition,

$$(5) \quad \log \lambda = \lim_{t \rightarrow \infty} E[(1/t) \log Y(t)].$$

The growth rate of the average population size is, by definition,

$$(6) \quad \log \mu = \lim_{t \rightarrow \infty} (1/t) \log E[Y(t)].$$

The only difference between these two quantities is the posi-

tion of  $E(\cdot)$ . In  $\log \lambda$ , the growth rate of each separate realization of the population is computed first (think of each realization as one computer simulation, or as one of a large number of demes), and then the growth rates are averaged. In  $\log \mu$ , the average population size at each time  $t$  is computed (averaged over all simulations or over all demes), and then the growth rate of the average is found. If the Leslie matrices  $L(t)$  do not vary at all, so that  $s_0(t)$  is actually constant, then the three measures, the median of  $\lim_{t \rightarrow \infty} (1/t) \log Y(t)$ ,  $\log \lambda$ , and  $\log \mu$ , are all identical to  $r$ .

In general, the exact computation of  $\log \lambda$ , even for independently distributed Leslie matrices with constant mean, is quite difficult (Cohen 1977a, 1979a), although we will find  $\log \lambda$  easily in a simple example in the next section. The computation of  $\log \mu$ , on the other hand, is generally easy, as we now show. Equation (1) implies that, given  $y(0)$ ,

$$(7) \quad y(t) = L(t)L(t-1) \dots L(2)L(1)y(0).$$

Take the average of both sides:

$$(8) \quad E[y(t)] = E[L(t)L(t-1) \dots L(2)L(1)]y(0).$$

Since successive Leslie matrices are independent, the expectation of the product is the product of the expectations; and since the mean of  $L(t)$  is identical over time,

$$(9) \quad E(L(t)L(t-1) \dots L(1)) = (E(L(1)))^t.$$

Substituting (9) into (8) gives

$$(10) \quad E[y(t)] = (E(L(1)))^t y(0).$$

Assuming that  $E(s_0(t)) > 0$ , so that on the average at least some eggs survive to age 1, and provided that the initial population is positive in all age classes,  $E[Y(t)]$  grows proportionally to  $\rho^t$  for large  $t$ , where  $\rho$  is the dominant eigenvalue of the average Leslie matrix  $E(L(1))$ . Consequently, for some constant of proportionality  $c$ ,

$$(11) \quad E[Y(t)]/(\rho^t) \rightarrow c \text{ for large } t.$$

Taking logarithms of both sides of (11), dividing by  $t$ , and letting  $t$  become large gives  $\log \rho = \lim (1/t) \log E[Y(t)]$ . Comparison with (6) shows that  $\rho$  must equal  $\mu$ , i.e. for this model,  $\mu$  is exactly the dominant eigenvalue of the average Leslie matrix  $E(L(1))$ .

The actual procedure to compute (6) is simple: when successive Leslie matrices are independently distributed with constant mean, take the average of the Leslie matrices (this means average each element of the matrix one at a time), find the largest eigenvalue of the matrix (using standard computer programs), take the natural logarithm of the eigenvalue, and the growth rate of the expected population size is found. Error estimates for  $\mu$  are derived below.

Since the logarithm is a concave function, i.e. its graph has decreasing slope,

$$(12) \quad \log \lambda \leq \log \mu$$

and the computation of (6) gives an upper bound for the value

of (5). This inequality (12) holds for any stochastic population model, not merely those analyzed here.

**Simple Example: One Reproductive Age Class**

To illustrate the computation of  $\log \lambda$  and  $\log \mu$  in a simple example, let us approximate the structure of the fish population by two age classes, so that we have only nonreproductive eggs and reproductive adults:

$$(13) \quad L(t) = \begin{pmatrix} 0 & E_1 \\ s_0(t) & 0 \end{pmatrix}.$$

(Here, we temporarily abandon the assumption, made in the previous section, that the effective fertility of the oldest age class, which is  $E_1$  in (13), is 0. If we did take  $E_1 = 0$ , the population would go extinct after 2 yr. But taking  $E_1 > 0$ , as we shall do in this section only, means that this year's eggs are produced by last year's adults, not by this year's adults. We accept this modification of the model described in the previous section in order to illustrate some calculations in a simple case.)

First, we shall compute  $\log \lambda$ . Notice that

$$(14) \quad L(2t)L(2t-1) = \begin{pmatrix} E_1 s_0(2t-1) & 0 \\ 0 & E_1 s_0(2t) \end{pmatrix}, t = 1, 2, \dots$$

which is nice because it is very easy to multiply diagonal matrices (a diagonal matrix has zero elements everywhere except possibly on the main diagonal): one simply multiplies corresponding diagonal elements. So we get, using (14) in (7),

$$(15) \quad \begin{aligned} y_0(2t) &= E\{s_0(1)s_0(3) \dots s_0(2t-1)y_0(0)\} \\ y_1(2t) &= E\{s_0(2)s_0(4) \dots s_0(2t)y_1(0)\}. \end{aligned}$$

Hence

$$(16) \quad \begin{aligned} (1/(2t)) \log y_0(2t) &= (1/2) \log E_1 \\ &+ (1/(2t)) \left[ \sum_{u=1}^t \log s_0(2u-1) + \log y_0(0) \right] \\ (1/(2t)) \log y_1(2t) &= (1/2) \log E_1 \\ &+ (1/(2t)) \left[ \sum_{u=1}^t \log s_0(2u) + \log y_1(0) \right]. \end{aligned}$$

For all  $\mu$ ,  $\log s_0(2\mu)$  and  $\log s_0(2\mu-1)$  are observed or sampled values of the same random variable  $\log s_0(t)$ , which we shall assign the same probability distribution as  $\log s_0(1)$ . Now we assume that  $E[\log s_0(1)]$  exists. Then, the strong law of large numbers applies to the right sides of (16) and implies that, with probability 1,

$$(17) \quad \begin{aligned} \lim_{t \rightarrow \infty} [2t]^{-1} \log y_0(2t) &= \lim_{t \rightarrow \infty} [2t]^{-1} \log y_1(2t) \\ &= (1/2) \log E_1 \\ &+ (1/2) E(\log s_0(1)). \end{aligned}$$

Since the almost sure limit is the same for  $y_0(t)$  and  $y_1(t)$ , it is the same for their sum. Consequently, the mean and median growth rates of the total population size (eggs plus adults) for large  $t$  are also the same:

$$(18) \quad \log \lambda = (1/2) \log E_1 + (1/2) E(\log s_0(1)).$$

This expression (18) for  $\log \lambda$  is valid if  $s_0(t) > 0$  are independently and identically distributed and if  $E(\log s_0(1))$  exists.

Now assume  $s_0(t)$  is approximately lognormally distributed, specifically,

$$(19) \quad s_0(t) = s e^{mz(t)}, t = 1, 2, \dots$$

where  $s$  is a positive constant and  $z(t)$  is a normally distributed random variable with mean 0 and variance 1 and independent from one time to another. Thus,  $mz(t)$  has mean 0 and variance  $m^2$ . This model (19) must be only an approximation because, when  $m > 0$ ,  $mz(t)$  has a positive probability of being larger than any fixed bound, so that  $s e^{mz(t)}$  has a positive probability of being larger than 1. This makes no sense if  $s_0(t)$  is to be interpreted as a survival proportion. We shall assume now (and later will actually observe) that the probability that  $s_0(t)$  exceeds 1 is small enough to be neglected.

If  $m = 0$ ,  $L(t)$  is constant with dominant eigenvalue  $(E_1 s)^{1/2}$  and we recover the deterministic intrinsic rate  $\log \lambda = r = (1/2) \log (E_1 s)$ . If  $m \neq 0$ , we obtain, by substituting (19) into (18),

$$(20) \quad \log \lambda = (1/2) \log (E_1 s) + (1/2) E(mz(1)) = r,$$

regardless of the value of  $m$ , because  $E(mz(1)) = 0$ . Thus, in this example, regardless of the variance of the randomly varying exponent in the survival of eggs, the mean growth rate of population size is identical to that of the deterministic population model of the same structure but with no variance in the survival of eggs.

Now we compute  $\log \mu$ . We shall use the standard facts that (Aitchison and Brown 1957)

$$(21) \quad E(e^{mz(t)}) = e^{(1/2)m^2}$$

and that the expectation of a product of independent random variables is the product of the expectations. Taking the average of both sides in (15) gives

$$(22) \quad \begin{aligned} E[y_0(2t)] &= E_1 s^t e^{tm^2/2} y_0(0) \\ E[y_1(2t)] &= E_1 s^t e^{tm^2/2} y_1(0) \end{aligned}$$

so that

$$(23) \quad \log \mu = (1/2) \log (E_1 s) + m^2/4.$$

Comparing (23) with (20) confirms the general inequality  $\log \mu \geq \log \lambda$ . In addition, we see that  $\log \mu$  is a linearly increasing function of the variance of the exponent  $mz(t)$  in the survival of eggs. In this example, when there is variation in the survival of eggs, the growth rate in the mean population size always exceeds the intrinsic rate of natural increase in the deterministic model of the same structure. However, if the

variation in the survival of eggs becomes too large, the specific model (19) becomes inappropriate because it permits  $s_0(t)$  to exceed 1 with nonnegligible probability.

As a check on the correctness of (23), we may apply the procedure described at the end of the previous section, without the necessity of relying on the explicit formula (15). The procedure says first to find the expected Leslie matrix:

$$(24) \quad E(L(t)) = \begin{pmatrix} 0 & E_1 \\ se^{m/2} & 0 \end{pmatrix}.$$

The largest eigenvalue is  $(E_1 s)^{1/2} e^{m/4}$ , and the logarithm of the eigenvalue is identical to (23).

Although this simple example is artificial, because it considers only one adult age class, it illustrates the meaning of  $\log \lambda$  and  $\log \mu$ . It also illustrates the relations between these measures of growth and the intrinsic rate of natural increase of a deterministic model.

Under the conditions of this example, the median value of  $\lim_{t \rightarrow \infty} (1/t) \log Y(t)$  is identical to  $\log \lambda$ ; in fact, all realizations except for a set of probability 0 have growth rates given by  $\log \lambda$ . More general conditions under which  $\log \lambda$  is the growth rate of almost all realizations of a product of random matrices are given by the pioneering paper of Furstenberg and Kesten (1960).

### Approximate Standard Deviation of the Estimate of a Growth Rate

We now return to the general model (1) and (2). Suppose that all the elements in the Leslie matrix (2), except  $s_0(t)$ , are known either exactly or with negligible uncertainty. Suppose  $s_0(1), s_0(2), \dots, s_0(N)$  are a sample of  $N$  observed values of  $s_0(t)$ . Let the sample mean be  $\bar{s}_0$  and the variance of the sample mean be  $\text{Var}(\bar{s}_0)$ . (Recall that the variance of the sample mean is the sample variance divided by  $N$ .) Here, we assume that  $\text{Var}(s_0(t))$  is independent of  $t$  in addition to assuming that  $E(s_0(t))$  is independent of  $t$ .

The sample mean Leslie matrix  $\bar{L}$  is obtained by replacing  $s_0(t)$  in (2) with  $\bar{s}_0$ . Let  $\hat{\mu}$  be the dominant eigenvalue of  $\bar{L}$ . This  $\hat{\mu}$  is the sample estimate of the dominant eigenvalue  $\mu$  of the expected Leslie matrix  $E(L(t))$ .

The purpose of this section is to derive an approximation to the variance of  $\log \hat{\mu}$ . Notice that the dominant eigenvalue  $\mu$  is a constant, not a random variable; variation in  $\hat{\mu}$  arises from the sampling variability of  $\bar{s}_0$  around its true mean  $E(s_0(t))$ .

Our approximation to  $\text{Var}(\log \hat{\mu})$  rests on the crude but commonly used Taylor series technique, and neglects the uncertainty in all other elements of  $L(t)$ .

Let  $f$  be the function that produces  $\log \mu$ , given  $E(s_0(t))$ , i.e.

$$(25) \quad \log \mu = f(E(s_0(t))).$$

This function is simply the log of the dominant eigenvalue of the matrix  $L(t)$  with  $s_0(t)$  replaced by  $E(s_0(t))$ . Thus

$$(26) \quad \log \hat{\mu} = f(\bar{s}_0).$$

Now, expand  $f(\bar{s}_0)$  in a Taylor series about  $f(E(s_0(t)))$  and drop all but the first two terms:

$$(27) \quad f(\bar{s}_0) = f(E(s_0(t))) + [\bar{s}_0 - E(s_0(t))](df/ds_0)_{s_0 = \bar{s}_0}.$$

Then subtract (25) from (26) and approximate  $f(\bar{s}_0)$  by its truncated Taylor series expression (27):

$$(28) \quad \log \hat{\mu} - \log \mu = [\bar{s}_0 - E(s_0(t))](df/ds_0)_{s_0 = \bar{s}_0}.$$

Square both sides of (28) and take expected values. Then assume  $E(f(\bar{s}_0))$  is close to  $f(E(s_0(t)))$ , which will asymptotically be true for large numbers of data points. We obtain

$$(29) \quad \text{Var}(\log \hat{\mu}) \sim E[(\log \hat{\mu} - \log \mu)^2] \\ = \text{Var}(\bar{s}_0)[(df/ds_0)_{s_0 = \bar{s}_0}]^2.$$

To compute  $df/ds_0$ , we can use formula (11) of Caswell (1978, p. 218):

$$(30) \quad (df/ds_0)_{s_0 = \bar{s}_0} = (d \log \mu / d \mu)(d \mu / d s_0)_{\mu = \hat{\mu}, s_0 = \bar{s}_0} \\ = u_1 v_0 / \hat{\mu}$$

where  $u$  is the left row eigenvector and  $v$  is the right column eigenvector corresponding to the dominant eigenvalue  $\hat{\mu}$  of  $\bar{L}$  and  $(u, v) = 1$ . The particular elements  $u_1$  and  $v_0$  appear because of the position of  $s_0$  in  $L$ . The easiest numerical method to compute the dominant eigenvalue of a Leslie matrix, namely the power method, produces  $u$  and  $v$  with no extra effort.

We shall illustrate the use of (29) below.

### Potomac River Striped Bass

In this section, we shall use data on the striped bass population that spawns in the Potomac River to test the model (1) and (2) and to illustrate numerically how to estimate  $\log \mu$ , the long-run rate of growth of the average population size.

A major assumption of the model (1) is that mortality is density independent. While this assumption is open to controversy in general, two lines of evidence make it plausible for the Chesapeake striped bass populations, including the population spawning in the Potomac River. First, in an analysis of the striped bass landings, Van Winkle et al. (1979) found a significant periodicity of 6 yr. This period length is not consistent with the period length that would be expected if the stock density were the causative agent (Van Winkle et al. 1979; Goodyear 1980). In addition, studies of the influence of environmental variables indicate that a large part of the annual variations in year-class strength are caused by variations in environmental factors, principally freshwater discharge and water temperature (Kohlenstein 1980; Ulanowicz and Polgar 1980). These observations indicate that the level of mortality is, at best, only weakly related to the size of the stock. We now proceed to a detailed analysis of data.

### THE DATA

We estimated  $F_i$ , the number of female eggs per female fish of age  $i$  for striped bass in the Chesapeake Bay, for  $i = 1, 2, \dots, 15$ , as shown in Table 1. These estimates are rounded to reflect the substantial uncertainty associated with them. The qualitative shape of the relation between age and female

TABLE 1. Estimated age-specific fecundity  $F_i$  of striped bass.

Age ( $i$ ) <sup>a</sup>	Fecundity ( $F_i$ ) <sup>b</sup>
1	0
2	0
3	0
4	33 000
5	170 000
6	350 000
7	530 000
8	680 000
9	900 000
10	1 000 000
11	1 200 000
12	1 500 000
13	1 800 000
14	2 100 000
15	2 400 000

<sup>a</sup>Age is measured in years since spawning.

<sup>b</sup> $F_i$  estimates the average fertile female eggs laid during the spawning season per female fish of age  $i$  as a function of age at maturity estimated by Merriman (1941) and estimated fecundity of mature females. Fecundity of mature females was estimated by converting lengths at annulus formation for females to weight (Mansueti 1961) and calculating the number of eggs using the weight–fecundity relationship reported by Jackson and Tiller (1952). The number of mature ova was then divided by 2 on the assumption that half would be females upon fertilization. Fecundities of ages 13–15 were estimated as the sum of the fecundity of the previous age plus the increment between the fecundity of age 11 and that of age 12.

eggs per fish is believed to be correct. We assume these data apply to the striped bass spawning in the Potomac River.

Since the fecundity estimates are uncertain, possible fluctuations in fecundity from year to year can be neither excluded nor measured. If present, they would contribute to variability in the number of eggs spawned via (32) below and hence via (33) to the estimated variability in the survival proportion of eggs. Thus, possible variations in fecundity may contribute to the estimated variability in the survival of eggs. In terms of the model (1) and (2), we take the number of post-egg age-classes to be  $k = 15$ .

Precise data on the age-specific survival proportions  $s_i$  are lacking. Different investigators report a substantial range of estimates of post-egg survival. We consider three sets of values for  $s_i$ , namely, for  $i = 1, \dots, 14$ ,  $s_i = 0.4$ ; or  $s_i = 0.5$ ; or  $s_i = 0.6$ . These three cases are chosen to cover most of the range of uncertainty about the true survival proportions. It will appear that the inferences to be drawn are insensitive to the value chosen for  $s_i$ . Calculations not presented here show that these inferences are also insensitive to minor refinements in the age distribution of mortality, e.g. to allow for a reported slightly increased mortality at ages 3–6 (Kohlenstein 1980; Polgar 1980). If, contrary to our assumption, the  $s_i$  are not constant in time, their fluctuations may contribute to the estimated variability in the survival of eggs in the same way that fluctuations in fecundity may, via (32) and (33).

Since  $E_i = s_i F_{i+1}$ , these assumptions plus Table 1 determine all the elements of the Leslie matrix  $L(t)$  in (2) except  $s_0(t)$ .

To estimate the distribution of the random variable  $s_0(t)$ ,

TABLE 2. Average catch (number of individuals of both sexes) per beach seine haul of fingerling striped bass in the Potomac River breeding site of Chesapeake Bay, based on annual surveys conducted by the Maryland Department of Natural Resources.

Year	Young-of-year <sup>a</sup>	Survival of eggs assuming adult survival $s_i$ is: <sup>b</sup>		
		0.4	0.5	0.6
1954	5.2			
1955	5.7			
1956	6.2			
1957	2.6			
1958	8.4			
1959	1.6			
1960	4.3			
1961	25.7			
1962	19.7			
1963	1.1			
1964	29.2			
1965	3.4			
1966	10.5			
1967	1.9			
1968	0.7			
1969	0.2			
1970	20.1	$9.34 \times 10^{-7}$	$2.98 \times 10^{-7}$	$1.06 \times 10^{-7}$
1971	8.5	$1.10 \times 10^{-4}$	$3.23 \times 10^{-5}$	$1.07 \times 10^{-5}$
1972	1.8	$5.83 \times 10^{-5}$	$1.59 \times 10^{-5}$	$4.92 \times 10^{-6}$
1973	2.1	$1.86 \times 10^{-5}$	$4.50 \times 10^{-6}$	$1.26 \times 10^{-6}$
1974	1.5	$3.58 \times 10^{-5}$	$7.39 \times 10^{-6}$	$1.80 \times 10^{-6}$
1975	7.7	$2.04 \times 10^{-5}$	$5.74 \times 10^{-6}$	$1.52 \times 10^{-6}$
1976	3.2	$6.33 \times 10^{-5}$	$2.13 \times 10^{-5}$	$6.82 \times 10^{-6}$
1977	1.9	$2.65 \times 10^{-5}$	$8.32 \times 10^{-6}$	$2.69 \times 10^{-6}$
1978	7.9	$2.11 \times 10^{-5}$	$5.84 \times 10^{-6}$	$1.78 \times 10^{-6}$
1979	2.1	$1.29 \times 10^{-4}$	$3.21 \times 10^{-5}$	$9.03 \times 10^{-6}$
1980	2.3	$3.73 \times 10^{-5}$	$9.82 \times 10^{-6}$	$2.70 \times 10^{-6}$
1981	1.4	$3.66 \times 10^{-5}$	$1.08 \times 10^{-5}$	$3.29 \times 10^{-6}$
1982	—	$2.45 \times 10^{-5}$	$7.05 \times 10^{-6}$	$2.13 \times 10^{-6}$

<sup>a</sup>Young-of-year  $t$  is taken as an index of  $y_i(t+1)$ , the number of 1-yr-old female fish at the time of the spawning season in calendar year  $t+1$ . Thus, the average catch of 2.3 individuals in 1980 indexes the 1-yr-old female population in 1981. (Data courtesy of Maryland Department of Natural Resources (B. Florence).)

<sup>b</sup>Survival of eggs  $s_0(t)$  from year  $t-1$  to year  $t$  is  $y_i(t)/y_0(t-1)$ , where  $y_0(t-1)$ , the number of eggs spawned in  $t-1$ , is calculated assuming that the post-egg annual survival of females is  $s_i$ ,  $i = 1, 2, \dots, 14$ .

we exploit the time series reported by Florence (1980) and supplemented subsequently by the Maryland Department of Natural Resources. Table 2 shows the average catch (number of individual male and female fish) per beach seine haul of fingerling striped bass in the Potomac River, based on a standardized seining procedure conducted in late summer and early autumn of each year by the Maryland Department of Natural Resources. We have not been able to determine the standard deviation, due to sampling variability, that should be associated with each of these average annual values. It is therefore not possible for us, at this time, to determine what biological significance should be attached to the differences between years in average catches. Thus, the following calculations should tentatively be treated as illustrative rather than as definitive.

It is possible that the Maryland Department of Natural

Resources will release more detailed data in the future. The need to make intelligent practical use of data such as those in Table 2 seems to us to justify the presentation of useful methods now.

Fingerlings are approximately 3–5 mo old and are assumed to have a sex ratio of approximately 1:1. We shall assume that the mortality between fingerling age and 1 yr of age is constant and therefore shall take the average number of fingerlings sampled in calendar year  $t$  as an index of the number  $y_1(t+1)$  of 1-yr-old female striped bass in the population in the following spring of year  $t+1$ ,  $t = 1954, \dots, 1981$ . The total number of fingerlings differs from the number of female yearlings only by a constant of proportionality, so no error will be introduced in the computation of  $s_0(t)$  (see (33) below).

#### CONSTRUCTING THE SPAWNING STOCK AND SURVIVAL PROPORTION OF EGGS

We now use this time series of  $y_1(t)$  in Table 2 plus the assumed post-egg survival coefficients to estimate the age structure of the post-egg population (i.e. the population aged 1–15 yr) for the years 1969–81. In 1969, the 1-yr-olds of 1955 (i.e. the fingerlings caught in 1954) who have survived will be 15, since  $1 + (1969 - 1955) = 15$ . Therefore, the expected number of 15-yr-olds in 1969 is  $y_{15}(1969) = y_1(1955)s_{15} \dots s_{14}$ . Similarly, the expected number of 14-yr-olds in 1969 is the number of 1-yr-olds in 1956 who have survived 13 yr, i.e.  $y_{14}(1969) = y_1(1956)s_{13} \dots s_{13}$ . In general, for  $t = 1969, \dots, 1980$ , the post-egg age structure is given by the data for 1-yr-olds and this computation for older fish:

$$(31) \quad y_i(t) = y_1(t-i+1)s_{i-1} \dots s_{i-1}, \quad i = 2, \dots, k.$$

We do not know the entire age structure prior to 1969 because we do not know the fingerling age-classes in years prior to 1954. Since the four oldest age-classes contribute approximately 3% to the net rate of reproduction of the population, one could approximate those four age-classes by a single age-class, without much loss in accuracy, in order to extend the time series of post-egg censuses for a few additional years. Computations not reported here suggest that combining the last few age-classes has little effect on the inferences that follow.

Given the post-egg age structure for  $t = 1969-81$ , we compute the expected number of eggs spawned in 1969 to 1981 by

$$(32) \quad y_0(t) = \sum_{i=1}^k F_i y_i(t), \quad t = 1969, \dots, 1981.$$

Then we compute the proportion of eggs surviving to 1 yr of age by the relation, which is a consequence of (1) and (2),

$$(33) \quad s_0(t) = y_1(t)/y_0(t-1), \quad t = 1970, \dots, 1982.$$

This computation is independent of the form of the probability distribution assumed for  $s_0(t)$ .

Although we started with a time series of data for finger-

lings from 1954 to 1981, we are left with an estimate of the 1-yr survival of eggs only for the years 1970–82 because of the long life and sustained fecundity of the striped bass. Figure 1 plots  $\log s_0(t)$  as a function of year  $t$  for each of the assumed values of  $s_i$ .

In linear regressions not reported here, we have investigated whether the proportion of eggs surviving, estimated from (33), appears to depend on the expected number of eggs spawned, estimated from (32). We found no significant evidence of density dependence in the survival of eggs.

#### IS THE SURVIVAL PROPORTION OF EGGS INDEPENDENTLY DISTRIBUTED WITH CONSTANT MEAN?

We now test the assumption that  $s_0(t)$  is distributed independently over time with constant mean. It is crucial to test this assumption before estimating  $\log \mu$  because the correctness of our method of estimation depends on this assumption. If  $s_0(t)$  is not independently distributed over time, the estimate of  $\log \mu$  obtained under the assumption of independence may be too high or too low. The more nearly independent  $s_0(t)$ , the better the estimation procedure that assumes independence.

The first test is visual inspection of Fig. 1. There appears to be no clear increasing or decreasing trend of  $\log s_0(t)$  as a function of  $t$ , for any value of  $s_i$ . There also appear to be no excessively long runs of data points above or below the regression line, nor any clear alternation above and below. The only possible suggestion of change over time may be in the variance of  $s_0(t)$ , which might decrease as time increases. We now test these observations more formally.

In the linear regression  $\log s_0(t) = a + bt$ , plotted in Fig. 1, the coefficient  $b$  and its standard deviation are  $0.095 \pm 0.089$ ,  $0.095 \pm 0.087$ , and  $0.089 \pm 0.086$ , corresponding to each of the values of  $s_i = 0.4, 0.5$ , and  $0.6$ . The point estimates of  $b$  do not differ significantly from 0 at the 0.25 level for any of these values of  $s_i$ . More importantly, 95% confidence intervals for  $b$  include a substantial range of both positive and negative values. To illustrate with  $s_i = 0.5$ , the data justify rejecting, at the 5% level of significance, an exponential increase in  $s_0(t)$  at a rate greater than  $0.095 + 1.96(0.087) = 0.266$  or roughly 27% per year or a decrease at a rate larger in magnitude than 8% per year. Thus, the data are consistent with a broad range of values of  $b$  including that assumed in (1),  $b = 0$ .

One might suspect that no real set of only 13 data points could provide significant evidence for a linear trend in  $\log s_0(t)$ . On the contrary, in work to be reported elsewhere, we find that at several Chesapeake Bay spawning sites other than the Potomac River, and in the bay as a whole, the correlation of  $\log s_0(t)$  with  $t$  is significantly negative (C. P. Goodyear, J. E. Cohen, and S. W. Christensen, unpublished data). For such populations, with declining survival of eggs, the present model and methods cannot be used directly.

The autocorrelations of the residuals from the above linear regression at lags 1, 2, and 3 are not significantly different from 0 (the maximum of the  $t$ -ratios was 1.9) and decline in magnitude with increasing lag. Thus, there is no significant evidence for correlations in survival over time.

To test whether the variance of  $\log s_0(t)$  changes over time, we computed the residuals of  $\log s_0(t)$  from the regression line

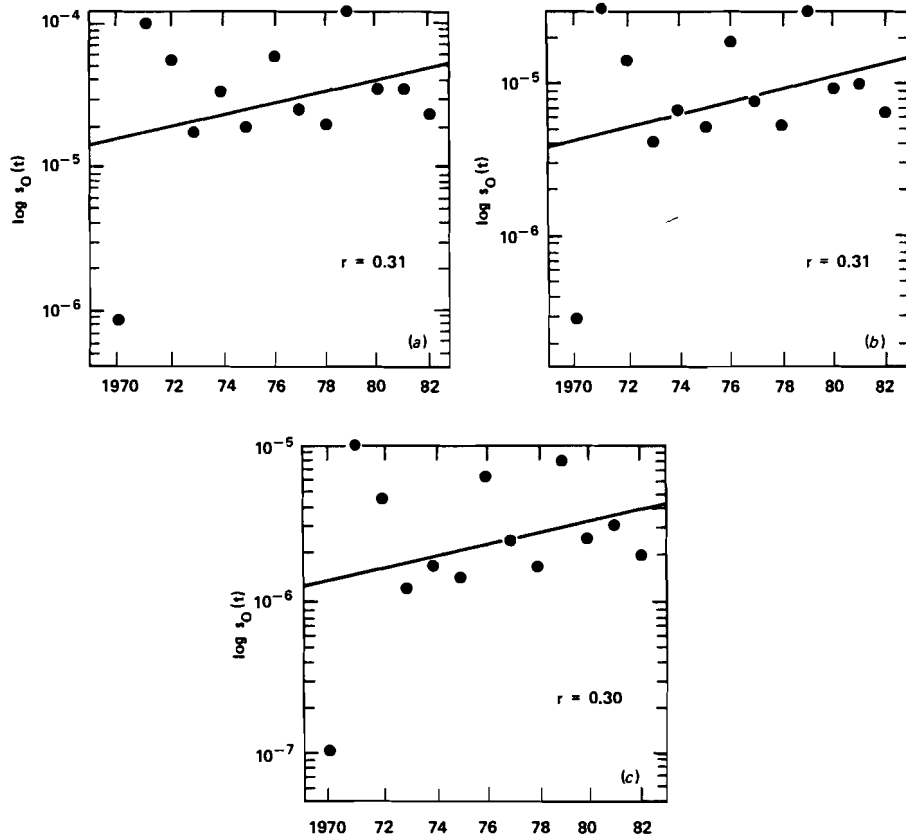


FIG. 1. Survival proportion of eggs to age 1 yr, plotted on logarithmic scale, from 1970 to 1982, at the Potomac River breeding site of the Chesapeake Bay striped bass at (a)  $s_i = 0.4$ , (b)  $s_i = 0.5$ , and (c)  $s_i = 0.6$ .  $r$ , linear correlation coefficient between the logarithm of the survival proportion and the year;  $s_i$ , assumed annual survival proportion of post-egg females.

$a + bt$ , took the absolute values of the residuals, and fitted a regression line of the form  $c + dt$  to the absolute values of the residuals. If the variance were independent of time,  $d$  would not differ significantly from 0. For all three values of  $s_i$ , the estimates of  $d$  fall between  $-0.11$  and  $-0.12$ , with standard errors between 0.047 and 0.051. The probabilities that  $d$  differs from 0 by chance alone, in a two-tailed test, all lie between 0.025 and 0.05. The variance of  $\log s_0(t)$  may change with  $t$ , but the evidence is not strong. The apparently large variance for early  $t$  arises from just two data points rather than from many.

The computation of  $\log \mu$  does not depend on whether the variance in survival of eggs is independent of time, but the approximation (29) to the variance of  $\log \mu$  does presume that  $\text{Var}(s_0(t))$  is independent of  $t$ .

We conclude that, for the Potomac River, the evidence against the assumption that  $s_0(t)$  is independently distributed over time with constant mean is statistically weak. Because of the limited number of years of observation, we do not exclude the possibility that the average  $s_0(t)$  increases by up to 26% or decreases by up to 8% a year. We also do not exclude the possibility that a lack of independence over time in the true

survival probabilities is masked statistically by large, independent sampling variation.

#### HOW IS THE SURVIVAL PROPORTION OF EGGS DISTRIBUTED?

Given that  $s_0(t)$  is approximately independently, and approximately identically, distributed over time, what is its distribution? This question arises because we want to test whether the sample mean  $\bar{s}_0$  differs significantly from the survival proportion  $s$  required for replacement, and it would be convenient to use a test based on statistical theory that presupposes a normal distribution.

We apply two tests of normality implemented in the program library SAS Version 79.5 at Stanford University's computing center: the test of Shapiro and Wilk (1965) (PROC UNIVARIATE) and the Kolmogorov-Smirnov test using Lilliefors' (1967) table of critical points for testing normality when mean and variance are estimated from the sample (PROC KSLTEST). According to Stephens (1974, p. 735), the Shapiro-Wilk statistic provides a more powerful test of normality when the mean and variance must be estimated from the data than the best known statistics based on the



empirical distribution function. This means that if data are non-normally distributed, the Shapiro–Wilk statistic will generally give a “more significant” result (a lower value of the probability  $P$  of the null hypothesis of normality) than will the Kolmogorov–Smirnov test. Our results from applying both tests to our data are consistent with Stephens’ finding.

For all three values of adult survival  $s_i$ , both tests reject the null hypothesis that  $s_0(t)$  is normally distributed at probability levels between 0.01 and 0.05. Normal probability plots (not shown here) appear curved. (They should be nearly straight for normally distributed data.)

The model (19) suggests that  $\log s_0(t)$  should be approximately normally distributed. The Shapiro–Wilk test rejects the normality of  $\log s_0(t)$  for all three  $s_i$  at probability levels less than 0.05. However, the Kolmogorov–Smirnov test rejects normality of  $\log s_0(t)$  at the 0.01 level when  $s_i = 0.4$  and fails to reject normality of  $\log s_0(t)$  at greater than the 0.10 level when  $s_i = 0.5$  and 0.6. Normal probability plots of  $\log s_0(t)$  (also not shown) appear more nearly straight. We infer that  $s_0(t)$  is more nearly lognormally distributed than normally distributed, but the fit to neither distribution is very good.

#### IS THE MEAN SURVIVAL PROPORTION OF EGGS DIFFERENT FROM THE PROPORTION REQUIRED FOR REPLACEMENT?

We can compute the proportion  $s$  of eggs that would have to survive to age 1 yr for the deterministic population with  $L(t)$  given by (2) and  $s_0(t) = s$  to be stationary (constant population in the long run). The value of  $s$  that gives the Leslie matrix a dominant eigenvalue of 1 may be computed by a formula of Van Winkle et al. (1974) and Vaughan and Saila (1976). The power method may be used to confirm that this value of  $s$  gives the Leslie matrix a dominant eigenvalue of 1. With adult survival  $s_i = 0.4$ , we found  $s = 6.93 \times 10^{-5}$ ; with  $s_i = 0.5$ , we found  $s = 2.11 \times 10^{-5}$ ; with  $s_i = 0.6$ , we found  $s = 6.82 \times 10^{-6}$ .

In the long run, the average population size  $E(Y(t))$  will increase or decline if and only if  $\log \mu > 0$  or  $\log \mu < 0$ , which in turn will hold if and only if  $E(s_0(t)) > s$  or  $E(s_0(t)) < s$ , in the model (1). We now test whether  $\bar{s}_0$ , the sample mean survival proportion of eggs and the maximum likelihood estimator of  $E(s_0(t))$ , differs significantly from the survival proportion  $s$  required for replacement.

For the cases  $s_i = 0.4, 0.5$ , and 0.6, the respective sample mean survival proportions  $4.48 \times 10^{-5}$ ,  $1.24 \times 10^{-5}$ , and  $3.75 \times 10^{-6}$  are all less than the respective survival proportions  $s$  required for replacement, namely,  $6.93 \times 10^{-5}$ ,  $2.11 \times 10^{-5}$ , and  $6.82 \times 10^{-6}$ , but the difference is less than one standard deviation, respectively,  $3.72 \times 10^{-5}$ ,  $1.02 \times 10^{-5}$ , and  $3.22 \times 10^{-6}$ . Regardless of distributional assumptions, the evidence that  $E(s_0(t))$  is less than  $s$  appears weak.

Since  $\log s_0(t)$  is approximately normally distributed (at least for  $s_i = 0.5$  and 0.6), it would be tempting to apply the  $t$ -test to the sample mean of  $\log s_0(t)$ . However, this would be equivalent to testing whether the geometric, and not the arithmetic, mean of  $s_0(t)$  differs from  $s$ , which is the wrong question.

In the appendix, an asymptotic likelihood ratio test is derived to test the null hypothesis that a sample of observations

comes from a lognormal distribution with fixed mean versus the alternative hypothesis that the observations come from a lognormal distribution with some other mean.

Here, the observations are  $s_0(t)$ ,  $t = 1970, \dots, 1982$ , and the fixed mean is the survival proportion  $s$  required for replacement, each calculated assuming the same value of the post-egg survival proportion  $s_i$ . For all three cases  $s_i = 0.4, 0.5$ , and 0.6, we find from (A6) that  $-2 \log LR$  is smaller than 0.8. The probability of a greater value of  $-2 \log LR$  by chance alone, assuming  $E(s_0(t)) = s$  and  $s_0(t)$  is lognormally distributed, exceeds 0.3. The data do not provide statistically significant evidence that the mean survival of eggs  $E(s_0(t))$  differs from  $s$ .

The test used is strictly valid only in the limit as the sample size approaches infinity; however, since the value of  $P$  is not on the borderline of significance, it seems safe to accept the conclusion of no significant difference between  $\bar{s}_0$  and  $s$  in this case. The conclusion that the average survival of eggs does not differ significantly from the deterministic level required to sustain a stationary population is robust with respect to the assumed value of the post-egg annual survival proportion  $s_i$ .

How might the conclusion of no significant difference between  $\bar{s}_0$  and  $s$  be affected if the young-of-year data in Table 2 add sampling variability to the biological variability? Substituting (31) into (32) and (32) into (33) shows that  $s_0(t)$  is a ratio of random quantities. The numerator is the observation at  $t$ . The denominator is a linear combination of observations prior to  $t$ . The variance of  $s_0(t)$  due to sampling and biological variation will be larger than the variance due to biological variability alone. A small real difference between  $E(s_0(t))$  and  $s$  may be masked if sampling variability inflates the estimated variance of  $s_0(t)$ . The conclusion of no statistically significant difference between  $\bar{s}_0$  and  $s$  must be regarded with substantial caution. Nevertheless, our finding (C. P. Goodyear, J. E. Cohen, and S. W. Christensen, unpublished data) of a statistically significant decline in  $s_0(t)$  with increasing time  $t$  at other spawning sites in the Chesapeake Bay shows that real biological trends can dominate whatever sampling variability there is in the young-of-year data and gives grounds for modest confidence in the results here.

#### GROWTH RATE OF MEAN POPULATION SIZE AND ITS APPROXIMATE VARIANCE

If there is no significant evidence that the mean annual survival proportion of eggs differs from that required for the population to be stationary in the long run, then an interval estimate of the growth rate  $\log \hat{\mu}$  of the average population size should include 0.

By way of illustration in the case  $s_i = 0.5$ , we find, from the power method, that the dominant eigenvalue of  $\bar{L}$  is  $\hat{\mu} = 0.927$  and  $\log \hat{\mu} = -0.076$ . Following the procedure under Approximate Standard Deviation of the Estimate of a Growth Rate, and thereby supposing that  $\text{Var}(s_0(t))$  is independent of  $t$ , we scale  $v$  so that its elements sum to 1 and obtain approximately  $u_1 = 10570$ ,  $v_0 = 0.99997$ ,  $\text{Var}(\bar{s}_0) = \text{Var}(s_0(t))/(13)^{1/2} = 2.89 \times 10^{-11}$ , and finally from (29),  $\text{Var}(\log \hat{\mu}) = 3.76 \times 10^{-3}$ . The standard deviation of the estimate  $\log \hat{\mu}$  is 0.061. The estimate  $\log \hat{\mu} = -0.076$  therefore differs from 0 by little more than one (approximate) standard deviation and has an approximate 95% confidence

interval from  $-0.198$  to  $+0.046$ . The absence of strong evidence here that  $\log \mu$  differs from 0 is consistent with the absence of strong evidence that  $E(s_0(t))$  differs from  $s$ . Because of sampling variability, the evidence is consistent with a substantial rate of decline or relatively small rate of increase in average population size.

When we introduced our numerical estimates of the presumably fixed parameters of the striped bass projection matrix  $L$ , we raised the possibility that both the post-egg survival proportions and adult fecundity may vary in time. What impact might such variations have on our point and interval estimates of  $\log \mu$ ?

Provided the variations in elements of  $L$  are independent over time, and provided our numerical estimates are the means of the corresponding random variables, the point estimate of  $\log \mu$  will be completely unaffected by the variation because  $\mu$  is the spectral radius of the mean matrix  $E(L(1))$ .

However, the approximate variance of  $\log \hat{\mu}$  in (29) is computed on the assumption that only  $s_0(t)$  varies, neglecting any other source of variation, and is proportional to the variance of  $\bar{s}_0$ . To the extent that (29) omits additional terms that reflect variation in elements of  $L$  other than  $s_0(t)$ , our approximate variance of  $\log \hat{\mu}$  is too small. In addition, since the estimate of  $s_0(t)$  from (31)–(33) omits any possible variation in  $s_i$  and  $F_i$ , our estimate of  $\text{Var}(\bar{s}_0)$  could also be too small. We conclude that our  $\text{Var}(\log \hat{\mu})$  from (29) will understate the actual variance of  $\log \hat{\mu}$  if post-egg survival and adult fecundity vary independently over time. A true interval estimate of  $\log \hat{\mu}$  would, in this case, be wider than that just estimated.

AVERAGE GROWTH RATE OF POPULATION SIZE

To estimate numerically  $\log \lambda$ , defined by (5), one procedure is to find the long-run invariant distribution of  $y(t)/Y(t)$  and use that to compute  $\log \lambda$  as the expectation of  $\log [Y(t+1)/Y(t)]$ . (Recall that  $y(t)$  is the age census, a vector, and  $Y(t)$  is the total population size, the sum of the elements of  $y(t)$ , at time  $t$ . Thus,  $y(t)/Y(t)$  is the normalized age census, i.e. the probability distribution of individuals according to age.) This procedure is described in Cohen (1977b, 1979b) and illustrated in Cohen (1977b, 1979c) for  $2 \times 2$  matrices. It does not appear to be practical for matrices as large as  $15 \times 15$ .

A second procedure would use the mathematical fact that, for any given sample path or simulation, as  $t$  gets large,  $(1/t) \log Y(t)$  approaches the right side of (5) with probability 1. We start a simulation from some arbitrary initial age census  $y(0)$ ; we use an initial age census with one individual in each age-class. To iterate (1), we specify  $L(t)$  by setting  $s_i = 0.5, i = 1, \dots, 14$ , and by choosing each value of  $s_0(t)$  from the corresponding column of Table 2 independently over time with probability  $1/13$ . For  $t$  equal to integer multiples of 20, we print the values of  $(1/t) \log Y(t)$ . Unfortunately, with a single simulation, one has no estimate of the variance of the estimator for, say, 1000 yr, namely  $(1/1000) \log Y(1000)$ , and running many simulations would be expensive.

In a third procedure, we take as  $y(0)$  a scalar multiple of  $y(400)$  obtained from a previous simulation. This choice eliminates any transient effects due to a possibly atypical initial age census. We iterate (1) exactly as above and at each step

compute

$$(34) \quad r(t) = \log [Y(t)/Y(t-1)], \quad t = 1, 2, \dots, 1000.$$

Then we take as our estimator the sample mean

$$(35) \quad \log \hat{\lambda} = (1/1000) \sum_{t=1}^{(1000)} r(t)$$

and compute the standard deviation of  $\log \hat{\lambda}$  in the ordinary way as the standard deviation of the sample mean of  $r(t)$ . We find  $\log \hat{\lambda} = -0.086$ . The standard deviation of  $\log \hat{\lambda}$  (not the standard deviation of  $r(t)$ ) is 0.0039. One can prove that, as the duration of the simulation (in this case, 1000) gets arbitrarily large, the sample mean of  $r(t)$  approaches  $\log \lambda$  with probability 1 and the standard deviation of this sample mean approaches 0. The inequality  $\log \hat{\lambda} = -0.086 < \log \hat{\mu} = -0.076$  is consistent with the inequality (12).

Although  $\log \hat{\lambda}$  is more than three standard deviations below 0, this is no evidence that  $\log \lambda < 0$ , because the estimator (35) takes as given the particular 13 values of  $s_0(t)$  on which the simulation is based. Even assuming that our model is correct, if we had happened to observe another 13 yr, we would have found different values of  $s_0(t)$  and a different estimate of  $\log \hat{\lambda}$ . An estimate of the variability of  $\log \hat{\lambda}$  that allows for the variation in  $s_0(t)$  could be computed using the jackknife or bootstrap (Efron 1982).

ROBUSTNESS OF CONCLUSIONS WITH RESPECT TO POSSIBLE OUTLIER

According to Fig. 1 and Table 2, the survival proportion of eggs in 1970 is notably lower than the survival proportion  $s_0(t)$  for all  $t$  after 1970. (It might seem paradoxical that  $s_0(1970)$  should be lower than all subsequent values of  $s_0(t)$  while the index of young-of-year caught in 1970 exceeds all subsequent indices of young-of-year. However, in (33), the numerator of  $s_0(1970)$ , namely  $y_1(1970)$ , is the index of young-of-year caught in the preceding calendar year, 1969, which is only 0.2, less than any subsequent value. The denominator of  $s_0(t)$  reflects the size of the spawning stock, which changes slowly over time compared with  $y_1(t)$ . It is therefore not surprising that  $s_0(1970)$  is lower than all subsequent values of  $s_0(t)$ .)

Here, we investigate whether the previous analyses would have reached different conclusions if this possibly exceptional point for 1970 had been omitted. In linear regressions of  $\log s_0(t)$  against  $t$  with 1970 omitted, the slope coefficient does not differ from 0 at the 0.5 level. For adult survival  $s_i$  of 0.4, 0.5, and 0.6, the slope coefficient and its standard error is  $-0.036 \pm 0.056, -0.029 \pm 0.058$ , and  $-0.029 \pm 0.062$ . Thus, 95% confidence intervals do not exclude both positive and negative slopes. The autocorrelations of the residuals from these linear regressions at lags 1, 2, and 3 are not significantly different from 0, for adult survival  $s_i = 0.4, 0.5$ , and 0.6. In regressions of the absolute values of the residuals against time, the slope coefficients do not differ significantly from 0 (the values of  $t$  are all less than 2). The corresponding values of the slope and its standard error are  $-0.028 \pm 0.031, -0.044 \pm 0.029$ , and  $-0.056 \pm 0.029$ . Thus, when 1970 is omitted, any suggestion that the variance of the residuals

declines with time is greatly weakened. We conclude that with 1970 omitted,  $s_0(t)$  is more nearly independently distributed over time with constant mean and constant variance.

With 1970 omitted, both tests of normality indicate that  $s_0(t)$  is not normal ( $P < 0.05$  for the Kolmogorov–Smirnov test and  $P < 0.02$  for the Shapiro–Wilk test, where  $P$  is the probability of the null hypothesis that  $s_0(t)$  is normally distributed) but that the normality of  $\log s_0(t)$  cannot be rejected ( $P > 0.15$  for the Kolmogorov–Smirnov test and  $P > 0.25$  for the Shapiro–Wilk test). Thus, the lognormal distribution describes acceptably the distribution of  $s_0(t)$  when 1970 is omitted, for  $s_i = 0.4, 0.5,$  and  $0.6$ .

To test whether the mean survival of these lognormal distributions differs from the mean survival proportion  $s$  required for replacement, we apply the likelihood ratio test from the appendix as before. For  $s_i = 0.4, 0.5,$  and  $0.6$ , the values with 1970 omitted of  $-2 \log LR$  and  $P$  are, respectively, 2.46 ( $0.1 < P < 0.25$ ), 3.19 ( $0.05 < P < 0.1$ ), and 3.42 ( $0.05 < P < 0.1$ ). We conclude, as before, that there is no strong evidence, even when 1970 is omitted, that the average survival of eggs differs significantly from the deterministic level required to sustain a stationary population.

We have shown that all our substantive conclusions are robust with respect to the unknown post-egg survival proportion  $s_i$  and with respect to the presence of a possible outlier, the data in 1970.

#### SUMMARY OF DATA ANALYSIS: PROCEDURE AND RESULTS

We summarize the major steps involved in estimating  $\log \mu$ , the long-run growth rate of average population size of an age-structured population with random survival of eggs to age 1 yr. We start with estimates of all elements of the Leslie matrix except the survival of eggs and a time series of the number of 1-yr-olds in the population. The time series must be significantly longer than the maximum reproductive age. We construct a time series of age censuses for the post-egg population, compute the number of eggs produced at each time for which we have a census, and by comparison of the number of eggs produced with the number of 1-yr-olds estimate the proportion of eggs that survive from one year to the next. The average of this survival proportion gives one element in the average Leslie matrix. The logarithm of the dominant eigenvalue of this average Leslie matrix gives  $\log \hat{\mu}$ , when the successive egg survival proportions are independently distributed with constant mean.

When performing this estimation procedure, it is crucial to test its assumptions against the data. Specifically, the assumption that the survival proportions are independently distributed over time with constant mean should be tested by all available means. If the survival proportions are used to make statistical inferences about whether the mean population size is changing the distributional assumptions underlying whatever statistical test is used should be checked and confirmed. Use of the estimation procedure without checking the assumptions that justify it may well mislead.

We also summarize the substantive conclusions we have reached about the striped bass population spawning in the Potomac River. On the basis of estimates of the age-specific fecundity of female fish and an assumed annual survival pro-

portion of post-egg fish equal to 0.5, the fraction of newly spawned eggs that must survive one year to maintain a stationary population is estimated at  $2.11 \times 10^{-5}$ . (As the post-egg annual survival proportion ranges from 0.4 to 0.6, the annual survival proportion of eggs that is necessary to maintain a stationary population ranges from  $6.93 \times 10^{-5}$  to  $6.82 \times 10^{-6}$ .) When the adult female stock is reconstructed from the survival of successive young-of-year cohorts, the input of eggs and hence the annual survival to yearlings can be estimated for each year. For annual post-egg survival proportions between 0.4 and 0.6, the annual proportion of eggs that survive to yearlings, denoted by  $s_0(t)$ , has a sample mean  $\bar{s}_0$  that is less than but does not differ significantly from the value required to maintain a stationary population. Provided that the variance of  $s_0(t)$  is not substantially inflated by sampling variability, and provided that the conditions that are assumed in our model were to continue to hold indefinitely, it would be statistically conservative to conclude that the asymptotic annual rate of change  $\log \hat{\mu}$  in the average size of populations statistically identical to that of the striped bass spawning in the Potomac River lies somewhere in the approximate 95% confidence interval from  $-0.198$  to  $+0.046$ . The average size may be decreasing by as much as 20% or increasing by up to 5% annually.

Recall from (12) that the almost sure growth rate ( $\log \lambda$ ) of any single population is always less than or equal to the growth rate of mean population size ( $\log \mu$ ). It would be ecologically and statistically conservative practice to continue sampling the young-of-year annually and to attempt to refine the estimates of post-egg survival and of adult fecundity in order to determine whether the suggestion of decline in the average population is happenstance or a genuine problem.

The assumption in our method to which our results are most vulnerable is that adult annual survival proportions and age-specific fecundities have been constant since 1954. Systematic changes in these parameters with time would cause bias in our estimates of  $s_0(t)$  that would increase with time.

For example, a trend of decreasing survival or decreasing age-specific fecundities of successive cohorts of adults with time would cause a systematic temporal bias in the ratio of the model-generated egg production to the real egg production. In this situation, the model egg production would overstate the true egg production and thereby underestimate egg survival by a greater fraction each year, which could result in a negative correlation of egg survival with time. Given the apparent increase in angler participation in the region over the period, a decline in the bass population, if found, could have been due entirely to increasing fishing mortality.

Systematic increases in survival or age-specific fecundities of successive cohorts would have the opposite effect. The true slopes of the regressions of egg survival against time would be decreased relative to those calculated if constant vital rates are assumed. The values of  $s_0(t)$  would be increasingly overestimated with time by our method. However, the true mean value of egg survival required for replacement would decrease, and its departure from the value  $s$  calculated assuming constant adult survival and fecundity would occur at a faster rate than the bias in the estimates of  $s_0(t)$  would increase with time. A decline in fishing mortality in response to declining stock would introduce this type of error in our

calculations. If some decline in fishing mortality and some increase in age-specific fecundity have occurred, actual egg survival has increased more slowly or has declined more than our analysis indicates, but the mean actual egg survival would still not be significantly below replacement.

### Use of These Methods in Environmental Impact Assessment

Mathematical models of population dynamics are central in attempts to evaluate the environmental impact of existing and proposed power plants (Christensen et al. 1976). Models serve to project the state of a population under baseline conditions, prior to plant operation, and under operating conditions. The difference between the baseline and operational projections describes the environmental impact of plants.

The mathematical models described here originated in a protracted regulatory struggle concerning the Hudson River (Christensen et al. 1981). Over a 17-yr period ending in 1980, Consolidated Edison, an electric utility supplying power to the New York City region, and other utilities, engaged in legal battle with the U.S. Environmental Protection Agency (Region II), the U.S. Nuclear Regulatory Commission, the Federal Energy Regulatory Commission, and a number of state agencies and citizens' groups over the effects of existing and proposed power plants on the Hudson River's fish populations, including the striped bass population.

Scientific consultants for the utilities proposed to evaluate the effects of plant operations by fitting a classical deterministic fish population model to time series of data on catch per unit effort. In the course of analyzing this aspect of the utilities' case, scientific consultants for the U.S. Environmental Protection Agency (Christensen et al. 1982) needed to use stochastic age-structured models. The methods described here offer analytically derived techniques, based on testable assumptions, for computing the long-run growth rate of the average population size when the age-specific vital rates are subject to random variations that are independently distributed over time with constant mean. This growth rate of average population size provides an upper bound on the average long-run growth rate of any single population subject to such random variations in age-specific vital rates.

We have applied these techniques to a time series of young-of-year catches per unit effort from the striped bass population spawning in the Potomac River, in conjunction with very approximate estimates of post-egg annual survival proportions and age-specific egg-laying rates. Although there is no statistically significant evidence that average population would, in the long run, be nonstationary, the data are so limited and variable that the average population may in fact be increasing or decreasing. The possibility of decline warrants continued surveillance of that fish population along with efforts to provide a firmer basis for the vital rates whose values now are largely surmised.

The methods described here, and the more general results referred to in the introduction, provide a framework for modeling stochastic variation of vital rates in real age-structured populations.

### Acknowledgments

J.E.C. held Fellowships from the John Simon Guggenheim Memorial Foundation, New York, the Center for Advanced Study in the Behavioral Sciences, Stanford, and the John D. and Catherine T. MacArthur Foundation, Chicago, during this work. His contribution was supported by National Science Foundation grant DEB80-11026 to Rockefeller University and by grants to the Center for Advanced Study from the National Institute of Mental Health (5T32MH14581-06) and the Exxon Education Foundation. S.W.C.'s contribution was supported by the U.S. Environmental Protection Agency, Office of Research and Development, Office of Environmental Processes and Effects Research, under Interagency Agreement EPA No. 79-D-X0533 with the U.S. Department of Energy (DOE No. 40-740-78), under contract W-7405-eng-26 with Union Carbide Corporation. We thank Lincoln Moses, D. L. DeAngelis, Lynn Gale, W. Van Winkle, D. S. Vaughan, and two insightful and constructive referees for helpful comments on earlier versions of the manuscript. Jean Hernandez typed the manuscript through many drafts.

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## Appendix

Likelihood ratio test for the mean of a lognormal random variable (derived by Lynn Gale, Center for Advanced Study in the Behavioral Sciences, 202 Junipero Serra Blvd., Stanford, CA 94305, USA).

We shall derive a test of the null hypothesis that  $n$  observed numbers  $x_1, x_2, \dots, x_n$ , are a random sample from the log-normally distributed random variable  $X$  with given mean  $E(X) = M$ , versus the alternative hypothesis that the observed numbers are a random sample from a lognormally distributed random variable  $X$  with some unknown mean other than  $M$ . Under both the null and the alternative hypotheses, the variance of  $X$  is assumed to be unknown.

Let  $Z = \log X$  and  $z_i = \log x_i$ ,  $i = 1, 2, \dots, n$ . Under the

alternative hypothesis, if  $Z$  is normally distributed with mean  $\mu$  and variance  $\sigma^2$ , the maximum likelihood estimators  $\hat{\mu}$  and  $\hat{\sigma}^2$  are, respectively,

$$(A1) \quad \hat{\mu} = \bar{z} \equiv \sum_{i=1}^n z_i/n$$

$$\hat{\sigma}^2 = \sum_{i=1}^n (z_i - \bar{z})^2/n.$$

It is important to observe the denominator  $n$  (not  $n - 1$ ) in  $\hat{\sigma}^2$ . Under the null hypothesis,

$$(A2) \quad M = \exp(\mu + \sigma^2/2) \quad \text{or} \quad \mu = \log M - \sigma^2/2$$

and we seek the maximum likelihood estimator  $(\sigma^*)^2$  of  $\sigma^2$  subject to this constraint (A2). The likelihood function for the observations is

$$(A3) \quad L = \prod_{i=1}^n ([2\pi]^{1/2} x_i \sigma)^{-1} \exp(-[z_i - \mu]^2 / [2\sigma^2]).$$

The maximum likelihood estimator  $(\sigma^*)^2$  is obtained by setting  $0 = \partial \log L / \partial \sigma$ . After some simplification we find

$$(A4) \quad (\sigma^*)^2 = 2[1 + \hat{\sigma}^2 + (\bar{z} - \log M)^2]^{1/2} - 2.$$

The likelihood ratio statistic  $LR$  is the quotient of the likelihood function of the sample given the constraint (A2) and using the estimator (A4) to the likelihood function of the sample under the alternative hypothesis using the estimators (A1):

$$(A5) \quad LR = \left[ \prod_{i=1}^n ([2\pi]^{1/2} x_i \sigma^*)^{-1} \exp(-[\log(x_i/M) + (\sigma^*)^2/2]^2 / [2(\sigma^*)^2]) \right]$$

$$\div \left[ \prod_{i=1}^n ([2\pi]^{1/2} x_i \hat{\sigma})^{-1} \exp(-[z_i - \hat{\mu}]^2 / [2\hat{\sigma}^2]) \right] \\ = (\hat{\sigma} / \sigma^*)^n \prod_{i=1}^n \exp(-[\log(x_i/M) + (\sigma^*)^2/2]^2 / [2(\sigma^*)^2] + [z_i - \hat{\mu}]^2 / [2\hat{\sigma}^2]).$$

Then, the log likelihood ratio statistic, defined to be  $-2 \log LR$ , will be large if it is much less probable that the sample is lognormally distributed with mean  $M$  than if the sample is lognormally distributed with some other mean. After some simplification, we find

$$(A6) \quad -2 \log LR = -2n(\log \hat{\sigma} - \log \hat{\sigma}^*) \\ - [\log M]^2 / [2(\sigma^*)^2] + \bar{z} \log M / (\sigma^*)^2 \\ + [\log M - \bar{z} + 1] / 2 - (\sigma^*)^2 / 8 \\ - [\hat{\sigma}^2 + \bar{z}^2] / [2(\sigma^*)^2].$$

Asymptotically (for large sample sizes),  $-2 \log LR$  has the distribution of  $\chi^2$  with one degree of freedom, so  $P$  values may be obtained from a table of the chi-squared distribution.