A STOCHASTIC MODEL FOR THE SIZE OF FISH SCHOOLS[1]

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ABSTRACT

A model is presented that reproduces the frequency distribution of fish school diameters observed acoustically in waters off southern California. The rate of change of school diameter is described by an equation that includes an entrance rate of fish into a school, which is independent of the number of fish in the school, and an exit rate, which is proportional to the number. The number in a school is assumed to be proportional to the square of the school diameter implying the average shape is disklike. Fluctuations in school size from unknown factors are approximated by stochastic rate terms for the entrance and exit rates and the diameter-number relation. This gives a stochastic dynamic equation for the rate of change of diameter and the probability distribution of the diameter is analyzed with a Fokker-Planck probability equation. A sensitivity analysis indicates two basic distribution types occur. Large exit rates and small stochastic fluctuations produce a narrow range of small diameters, while large entrance rates and large fluctuations produce a wide range of large diameters. Qualitative inferences from the model indicate schools of large fish should have a wide range of large diameters while small fish should have a narrow range of small diameters. Also fishing activity could decrease entrance rates and increase exit rates, and the combination would shift the probability distribution to a narrow range of small diameters.

When fish are mutually attracted they form schools, either in random orientation or in highly organized structures (Shaw 1978). The shape of the schools are diverse and changeable, and typically range from ribbonlike to spherical with the latter being uncommon (Radakov 1973). The attraction is mostly keyed visually and in northern anchovy, *Engraulis mordax*, schools off southern California the shape is disklike during the day and generally more diffuse and elongated at night (Squire 1978). Often within a school fish arrange in a lattice structure with the density of fish per unit volume related to fish length (Breder 1976; Serebrov 1976).

Models for the interactions of fish in a school have been postulated by a number of authors (see Breder 1976 for review and Okubo et al. 1977), but the processes controlling the size of a school in terms of the number of fish in a school or its physical dimensions have not been considered in mathematical terms. Considering what factors may be important in controlling size it is apparent the problem is complex and could include species behavior, light, predator-prey interactions, turbulence, life cycle stages, the stock population, and the size of the schools themselves.

An interesting set of observations on the size-frequency distribution of unidentified schools off southern California, shows a well-defined peak frequency at a diameter of about 15 m (Smith 1970). Towards larger and smaller diameters the frequency distribution decreases in an exponentiallike manner (Figures 1, 2).

This simple, and relatively stable, distribution is particularly interesting considering the possible complexity of the schooling process. The observations might be produced in one of two funda-

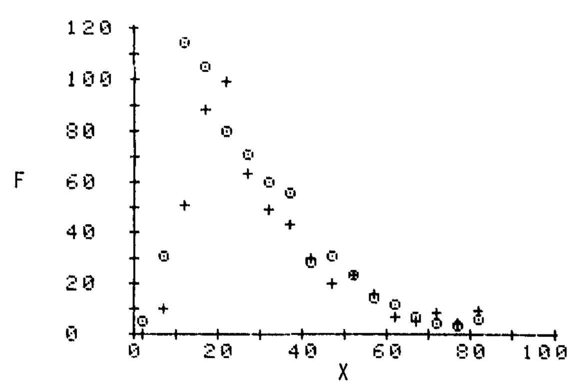

FIGURE 1.—Frequency distribution of fish schools (F) vs. school diameter (X) for unidentified schools observed with sonar by Smith (1970) from San Francisco, Calif., to Cabo San Lazaro, Baja California, in May 1969 (⊙) and June 1969 (+). F in numbers of schools and X in meters.

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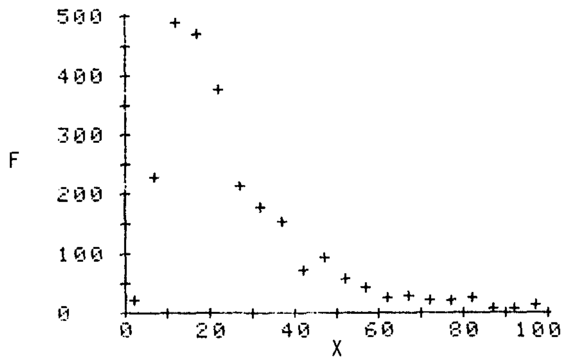

FIGURE 2.—Frequency distribution of fish schools (F) vs. school diameter (X) for composite of Smith's (1970) sonar surveys off California and Mexico in January, February, April, May, June, and July 1969.

mental ways. Either the frequency distribution is coupled to the school size or it is coupled to other factors such as the species composition of the observations. In the first case, the factors relating to environmental conditions, species, and stock numbers may also be acting on the school size but could be hidden in the averaging, inherent in the frequency mode of data display. In the second case, size may be insignificant and the distribution might reflect other factors. For example, if each species has a preferred school size, then a particular frequency distribution of species could produce an apparent frequency size correlation.

In this paper I explore the situation where the schooling dynamics are dependent on the school size and other factors, like species composition, have effects randomly distributed over the range of school sizes.

OBSERVATIONS

Smith (1970) observed fish schools over a 200,000 nmi^2 area between San Francisco, Calif., and Cabo San Lazaro, Baja California. The targets were recorded using sonar with a transducer fixed at a 90° relative bearing giving a beam perpendicular to the path of the ship. A 30 kHz frequency was used with a 10° conic beam (at −3 dB), at ranges from 200 to 450 m from the ship. Observations were made during daylight hours only and a complete survey of the area could be made in <2 mo. The dimensions of the schools were measured at right angles and parallel to the ship and the number of schools in 5 m intervals of diameter was estimated, correcting for bias from schools that only fell partially within the 200-450 m observation window of the sonar.

Frequency distributions for surveys in May and June 1969 were composed of 525 and 650 observations, respectively, in the diameter range 0-99 m (Figure 1). A composite frequency distribution of surveys in January, February, April, May, June, and July 1969 contained 2,549 observations of schools between 0 and 99 m diameter (Figure 2).

Smith (1970) estimated to a first order that about 30% of the observed schools were adult northern anchovy. Other common schooling fish in the area, the CalCOFI area, include northern anchovy juveniles; jack mackerel, *Trachurus symmetricus*, juveniles; Pacific bonito, *Sarda chiliensis*; Pacific mackerel, *Scomber japonicus*; and Pacific sardine, *Sardinops sagax*.

THE MODEL

To describe the frequency distribution of school diameters first consider an equation for the rate of change of the number of fish in a school. Define this rate in terms of a deterministic equation, which is related to school size, plus a stochastic equation which is taken to approximate the remaining unknown fluctuating behavior of the rate. The deterministic and stochastic equations are combined to give a stochastic dynamic equation for the rate of change of fish in a school as

$$\frac{dN}{dt} = \alpha + \delta(t) - \beta N + \gamma(t)N. \qquad (1)$$

The number of fish in a school is N and its change with time is determined as the difference between the rate fish enter the school, which is independent of N, and the rate fish exit from the school, which is proportional to N. The deterministic entrance and exit rates are α and βN where α and β are constant and represent averages over an ensemble of schools. The stochastic entrance and exit rates are $\delta(t)$ and $\gamma(t)N$ where $\delta(t)$ and $\gamma(t)$ represent white noise fluctuations which vary rapidly compared with variations in N, and are not affected by past conditions. The mean values of the stochastic terms are zero and so the stochastic parts represent fluctuations about the deterministic rate terms.

To express the frequency distribution in terms of school diameters we note Squire's (1978) observations in which the average shape of northern anchovy schools during the daylight hours is disklike. Including unknown factors that alter the three-dimensional shape through a stochastic term the relation between the school diameter and number is expressed as

$$N = X^2 (\rho + \epsilon(t)) \ \pi/4 \tag{2}$$

where X is the diameter of a school with a disklike shape, ρ is the average density of fish per unit horizontal area, and $\epsilon(t)$ is the stochastic variation on the density and has white noise character. Rewrite Equation (2) as

$$N = pX^2 (1 + h(t)) \tag{3}$$

where p is a generalized density with $p = \rho\pi/4$ and $h(t)$ is the stochastic density normalized to p giving $h(t) = \epsilon(t)/p$.

Using Equation (3) in Equation (1) and differentiating yields

$$\frac{dX}{dt} = \frac{\alpha}{2pX(1 + h(t))} - \frac{\beta X}{2} + \frac{\delta(t)}{2pX(1 + h(t))} + \frac{\gamma(t)X}{2} + \frac{dh(t)/dt}{2(1 + h(t))} . \tag{4}$$

To separate the deterministic and stochastic parts of Equation (4) assume $\rho > |\epsilon(t)|$ so $h(t)^2 < 1$ giving the convergent series

$$\frac{1}{1 + h(t)} = 1 - h(t) + h(t)^2 - h(t)^3 + \ldots = 1 + \sum_{m=1}^{\infty} (-h(t))^m . \tag{5}$$

Using Equation (5) in Equation (4) and separating deterministic and stochastic parts in powers of X yields the stochastic dynamic equation for X as

$$\frac{dX}{dt} = \frac{\alpha}{2pX} - \frac{\beta X}{2} + \frac{i(t)}{2pX} + \frac{j(t)X}{2} . \tag{6}$$

The first term on the right side of Equation (6) is the deterministic expansion rate of a school and the second term is the deterministic contraction rate. The third term is the stochastic expansion rate and is principally related to the stochastic entrance rate. The stochastic component in expanded form is

$$i(t) = \delta(t) + (\alpha + \delta(t)) \sum_{m=1}^{\infty} (-h(t))^m .$$

The last term in Equation (6) is the stochastic contraction rate and is related to the stochastic exit rate according to the relation

$$j(t) = \gamma(t) + \frac{dh(t)}{dt} \sum_{m=0}^{\infty} (-h(t))^m .$$

We assume the components $i(t)$ and $j(t)$ are stationary random processes with zero mean values. Then their statistics can be characterized by the relations

$$\overline{i(t)i(t + t')} = \sigma_i^2 \, q_i(t')$$

$$\overline{j(t)j(t + t')} = \sigma_j^2 \, q_j(t') \tag{7}$$

where σ^2_i and σ^2_j are positive constants that quantify the level of the stochastic inputs and are referred to as "incremental variances." The $q(t')$ terms are autocorrelation functions that quantify the spectrum characteristics of the stochastic inputs as a function of separation time t'.

To investigate the probability characteristics of X in Equation (6) we must combine the stochastic terms into a single stochastic input, in a manner that retains the statistical characteristics of the terms. From Equation (7) we define the ratio

$$r(t')^2 = \frac{\overline{i(t)i(t + t')}}{\overline{j(t)j(t + t')}} = \frac{\sigma_i^2 \, q_i(t')}{\sigma_j^2 \, q_j(t')} .$$

We assume the correlation functions are similar enough to make the simplification $q_i(t')/q_j(t') \approx 1$. Then we relate the two stochastic terms in Equation (6) as

$$i(t) = rj(t) \tag{8}$$

where r is the ratio of the intensities of the inputs and is defined as

$$r = \sigma_i/\sigma_j . \tag{9}$$

In effect with Equations (8) and (9) we are taking the ratio of the two stochastic terms to be equal to the ratio of their "incremental standard deviations." These are not the typical standard deviations, but if the correlation functions q_i and q_j are similar the ratio of the incremental standard deviations should approach the ratio of the typical standard deviations of the variables, i.e., $r \to \mathrm{SD}(i(t))/\mathrm{SD}(j(t))$ as $q_i(t')/q_j(t') \to 1$.

Now the stochastic dynamical equation for fish school diameter is written

$$\frac{dX}{dt} = \frac{\alpha}{2pX} - \frac{\beta X}{2} + \frac{j(t)}{2}\left[\frac{r}{pX} + X\right]. \quad (10)$$

The probability characteristics of X can be analyzed according to the Fokker-Planck equation (Goel and Richter-Dyn 1974). This is also known as the forward diffusion equation for probability in X and t. The probability density for the system having a diameter X at time t when it had diameter Y at time zero is denoted $P(X/Y,t)$ and for Equation (10) the Fokker-Planck equation is

$$\frac{\partial P(X,t)}{\partial t} = -\frac{1}{2}\left\{\frac{\partial}{\partial X}\left[\left[\frac{\alpha}{pX} - \beta X + \frac{\sigma^2}{8}\frac{\partial}{\partial X}\left(\frac{r}{pX}+X\right)^2\right]P(X,t)\right]\right\} + \frac{\sigma^2}{8}\frac{\partial^2}{\partial X^2}\left(P(X,t)\left(\frac{r}{pX}+X\right)^2\right). \quad (11)$$

The term σ^2 is the incremental variance of the diameter shrinkage rate and is in fact equivalent to σ^2_j in Equation (7). The term has a dimension of t^{-1} and is also the diffusion coefficient of probability $P(X,t)$ in X space. In this manner it quantifies the level of randomness in the schooling process.

For the Fokker-Planck equation the growth rate of the mean value of X is

$$M_1(X) = \frac{\alpha}{2pX} - \frac{\beta X}{2} + \frac{\sigma^2}{2}(r/pX + X)(1 - r/pX^2) \quad (12)$$

and the growth rate of the variance of X is

$$M_2(X) = \frac{\sigma^2}{4}(r/pX + X)^2. \quad (13)$$

From the similarity of frequency distributions for different months (Figures 1, 2) we assume a steady-state probability distribution and from Goel and Richter-Dyn (1974) this is expressed as

$$P(X) = \frac{C}{M_2(X)}\exp\left\{\int_0^X 2\frac{M_1(s)}{M_2(s)}\,ds\right\} \quad (14)$$

where C is a constant determined by the condition that the total probability equals one

$$1 = \int_0^\infty P(X)dX. \quad (15)$$

Using Equations (12) and (13) in Equation (14) the steady-state probability distribution, or probability density, for school diameter is

$$P(X) = \frac{kXe^{-2(a+bc)/(c+X^2)}}{(c+X^2)^{(1+2b)}} \quad (16)$$

where

$$a = \alpha/p\sigma^2,\ b = \beta/\sigma^2,\ c = r/p,$$
$$k = 4C/\sigma^2. \quad (17)$$

The dimensions of the above constants with l for length, t for time, and n for number of fish are as follows. The parameters a and c have dimensions of l^2, b is dimensionless, and k has dimensions of l^{1+4b}. The dimension of α is lt^{-1}, β and σ^2 have t^{-1}, p has nl^{-2}, r has n, and C has $t^{-2}l^{1+4b}$.

FITTING THE MODEL TO DATA

Equation (16) can be fit to Smith's (1970) data through a number of methods all of which adjust the free parameters a, b, and c to obtain a best fit according to visual or statistical criterion. To obtain a first order estimate of the free parameters we will use a simple algorithm in which the probability curve is made to go through the observed probability distribution at the most common, or peak, diameter and one other diameter in the distribution. This fixes two of the free parameters and with trial values of the remaining free parameter the model is fit to observations.

We begin by converting the probability equation to the frequency equation

$$F(X) = \frac{k^*}{k} P(K) \tag{18}$$

where $F(X)$ is the number of fish observed at diameter X and k^* is a constant that is a function of the number of schools observed. At the most common diameter X_0, the frequency is maximum so $dF(X_0)/dX = 0$ and from Equations (16) and (18) we obtain

$$a = X_0^2 \left(b + \frac{1}{4}\right) - \frac{1}{4} c^2/X_0^2. \tag{19}$$

With Equation (19) in $F(X)$ the log of $F(X)$ yields equations for b and k^*. These can be solved explicitly with observations $F(X_0)$, $F(X_1)$, X_0, X_1, and the free parameter c where X_1 is a diameter greater than the peak diameter X_0. The equations are

$$b = \frac{A(X_1) - A(X_0) + C(X_1) - C(X_0)}{B(X_1) - B(X_0)} \tag{20}$$

$$k^* = \exp\left\{-A(X_0) + bB(X_0) - C(X_0)\right\} \tag{21}$$

where
$$A(X_i) = \frac{1}{2}(c^2/X_0^2 - X_0^2)/(c + X_i^2) + \ln(X_i/(c + X_i^2)$$

$$B(X_i) = 2(c + X_0^2)/(c + X_i^2) + 2\ln(c + X_i^2)$$

$$C(X_i) = -\ln(F(X_i))$$

with $i = 0$ and 1.

For the composite of observations depicted in Figure 2 we take $X_0 = 14$ m, $X_1 = 40$ m, $F(X_0) = 491$, and $F(X_1) = 115$. A good fit (Figure 3) is obtained with $c = 60$ m^2 and the remaining constants from Equations (19), (20), and (21) are $a = 133$ m^2, $b = 0.452$, and $k^* = 4716244$.

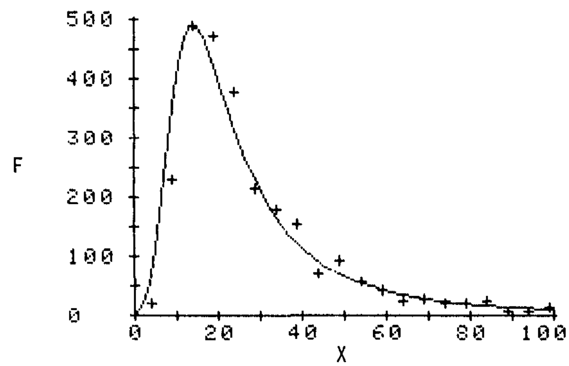

FIGURE 3.—Fit of probability equation of school diameter to frequency distribution of Figure 2. Probability Equation (16) is equated to frequency according to Equation (18).

SENSITIVITY ANALYSIS

The sensitivity of $P(X)$ to variations in the model parameters has been investigated for $P(X)$ in the configuration of the observed distribution (Figure 3).

We note that the curve $P(X)$ is defined by three free parameters a, b, and c which are in effect fitting parameters. These are ratios of the coefficients of the stochastic dynamic Equation (10). The coefficients are the dynamic parameters of the system and are α, β, σ, σ_i, and p. The relationship between the fitting parameters and the dynamic parameters is given by Equation (17) where σ_i is related to r by Equation (9). Because the dynamic parameters are only known in ratios in this model we can only investigate their effect on $P(X)$ in terms of relative changes. The relative value y', of a dynamic parameter y, can be defined

$$y' = y/y_o \tag{22}$$

where y_o is the value of the dynamic parameter corresponding to the fit to the observed frequency distribution.

To investigate the equation sensitivity, each dynamic parameter is varied while the others are held constant at their y_o values. For each set of dynamic parameters generated in this manner $P(X)$ is calculated for X from 0 to 100 m. For each set of parameters the constant k in Equation (16) is determined according to the condition expressed by Equation (15) by numerically integrating the integral

$$1/k = \int_0^{X^*} \frac{Xe^{-2(a+bc)/(c+X^2)}}{(c+X^2)^{(1+2b)}}\,dX. \qquad (23)$$

Using Simpson's rule for integration $1/k$ is evaluated within a few percent accuracy with a 1 m integration step and $X^* = 300$ m.

The response of $P(X)$ to variations in the dynamic parameters is illustrated in Figures 4-8,

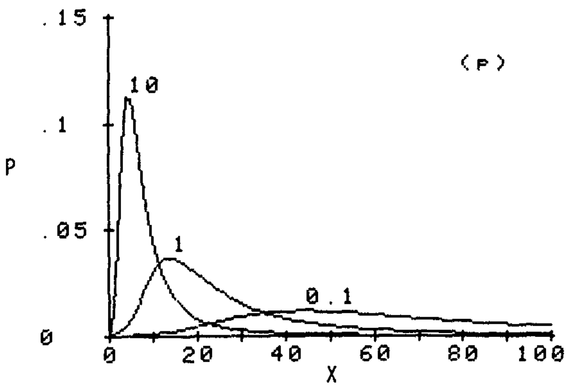

FIGURE 4.—Probability distribution (P) vs. school diameter (X), in meters, for relative schooling density parameter values p′ = 0.1, 1, and 10.

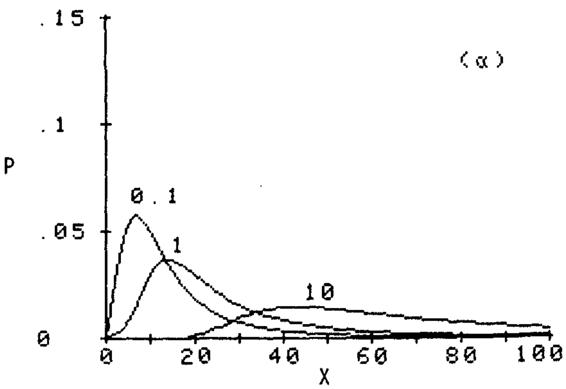

FIGURE 5.—Probability distribution (P) vs. school diameter (X) for relative entrance rate values $\alpha' = 0.1$, 1, and 10.

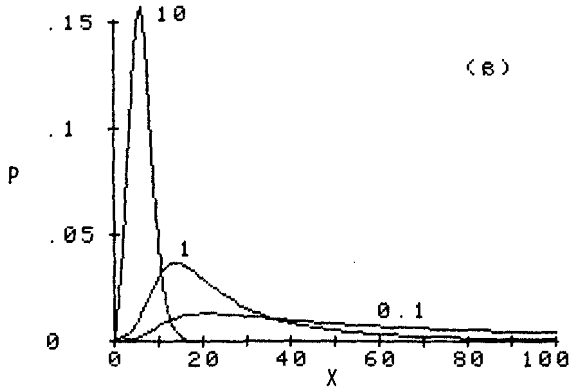

FIGURE 6.—Probability distribution (P) vs. school diameter (X) for relative exit rate parameter values $\beta' = 0.1$, 1, and 10.

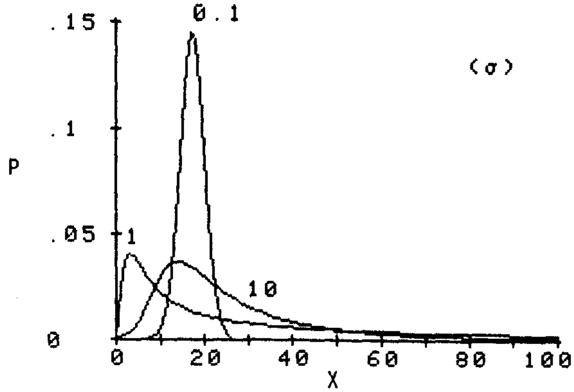

FIGURE 7.—Probability distribution (P) vs. school diameter (X) for relative shrinkage rate standard deviation values $\sigma' = 0.1$, 1, and 10.

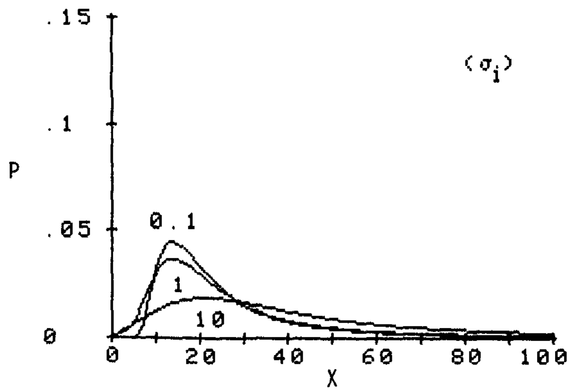

FIGURE 8.—Probability distribution (P) vs. school diameter (X) for relative expansion rate standard deviations values $\sigma'_i = 0.1$, 1, and 10.

which show $P(X)$ vs. X for each parameter varied with relative values $y' = 0.1, 1, 10$, where $y' = 1$ is the relative value corresponding with the fit to the observed distribution (Figure 3). In the figures the shape of $P(X)$ varies between a well-defined sharp peak, in which only a narrow range of diameters are probable, and a broad low peak, in which a larger range of somewhat larger diameters are probable. A brief discussion of the sensitivity and some possible biological implications follows.

p

The density, or number of fish per square meter of horizontal area of a school, has a strong effect on the probability distribution (Figure 4). A dense grouping of fish, corresponding with large values of p, favors a narrow range of small school diameters while a low density favors a wide range of larger diameters. Serebrov (1976) illustrated that the density of fish in a school is highly correlated to fish length according to the relation $\rho = 1/(LK)^3$ where ρ is the density in number of fish per cubic meter, L is fish length in centimeters, and K is a constant, with average value 2.44. If we assume the density per square meter is proportional to the density per cubic meter, then with Serebrov's relation, p responds to the one-third power of fish length averaged over the ensemble of schools making up the observations. Fish length becomes a sensitive parameter, e.g., the relative change in p from 1 to 10 in Figure 4 corresponds to a relative change in the average fish length from 1 to 0.46.

α

For small values of the entrance rate into schools, small diameters are favored, and as the entrance rate increases a wide range of large schools is favored (Figure 5).

The rate α has units of number of fish entering the school per unit time, and if we envision the entrance event as the chance encounter and joining of two schools, then α should be proportional to the average number of fish in the schools divided by the average time interval between encounters of schools. The time interval between encounters could decrease as the stock population increases if the number of schools per unit area increases. Thus, the entrance rate could increase with increases in the stock population of an area. This reasoning suggests that larger stocks would contain a wide range of school sizes and small stocks would contain a narrow range of small school sizes.

β

The parameter β is the coefficient for the average exit rate of fish from a school and has units of t^{-1}. If we envision the loss mechanism as a random dividing of the school into two fractions, with the time interval between the divisions being random, then the average time interval is proportional to β^{-1}. Thus, larger values of β correspond to short time intervals between divisions and small values correspond to large time intervals between school divisions. The interval as expressed by β has a significant effect on the probability distribution $P(X)$, with small values favoring a narrow range of small diameters and large values favoring a wide range of larger diameters (Figure 6).

σ

The randomness in the schooling process is quantified in the model by the incremental standard deviation σ, which has units of $t^{-1/2}$. For small levels of randomness, small σ, the probability distribution converges on the deterministic steady-state diameter which is defined

$$\bar{X}_0 = (\alpha/p\beta)^{1/2} = (a/b)^{1/2}.$$

For the model fit this gives $\bar{X}_0 = 17.3$ m. The convergence is evident in Figure 7 in which X_0 changes from 3 to 14 to 17 with σ changing from 10 to 1 to 0.1. At larger values of σ the system has more random character and the probability distribution spreads away from the deterministic value $\bar{X}_0$. Expressed as the incremental variance σ^2, with the dimension t^{-1}, the term is the diffusion coefficient of probability in X space, since the Fokker-Planck equation is in fact a diffusion equation of probability in X and t.

σ_i

The incremental standard deviation of the expansion rate, σ_i is defined by Equation (7) and is related to the probability equation through r according to Equation (9). It has a small effect on the probability distribution with larger values producing a broadening of the probability distribution and a shift towards larger diameters. Increasingly, smaller values asymptotically approach a stable distribution as is evident by the similarity of the curves for relative values $\sigma_i = 0.1$ and 1 (Figure 8).

DISCUSSION

The frequency distribution of fish school diameters observed acoustically off the coast of southern California by Smith (1970) has a well defined most frequent, or peak, diameter. The distribution is also skewed towards small diameters and is relatively stable from one month's observations to the next. These data likely represent a range of fish sizes and species with northern anchovy probably being the dominant group.

The frequency distribution can be modeled by a probability equation that is based on a dynamic equation that contains deterministic and stochastic rates for the entrance and exit of fish from a school. The entrance rates are taken to be independent of the number of fish in a school while the exit rates are taken to be proportional to the number. The number of fish in a school is transformed to a diameter by assuming the average school shape is disklike so the number is proportional to the horizontal area, as expressed by the square of the diameter.

The effects of environmental conditions, fish sizes, species, predator-prey interactions, and stock size are assumed to be contained in the stochastic parameters of the dynamic equation. This assumption requires these basically unknown factors have white noise character.

In effect the deterministic behavior of the rate of change of diameter is represented by a dynamical equation, $dx/dt = f(x)$, where $f(x)$ is the deterministic rate and is a function of x. The remaining unknown fluctuating behavior, due to other factors, is approximated by $e(x)j(t)$ where $j(t)$ is white noise fluctuation and $e(x)$ gives the x dependence of the stochastic rate. Combining the rates we obtain a dynamical stochastic equation for x and the probability analysis of the process can be carried out using a Fokker-Planck equation, which is a diffusion equation for probability in x and t. The solution of the Fokker-Planck equation gives the probability curve $P(X)$.

Fitting the curve $P(X)$ to Smith's (1970) observations yields the equation constants or fitting parameters a, b, and c. These fitting parameters are ratios of the dynamic parameters of the dynamical stochastic equation for x.

The sensitivity analysis of $P(X)$ to relative changes in the dynamic parameters indicates two basic probability distributions can be produced: 1) a narrow probability distribution, favoring a narrow range of small diameters with the occurrence of large schools unlikely and 2) a wide distribution in which a wide range of larger diameters have low but essentially equal probabilities, and small diameters are unlikely. Wide distributions are favored by large entrance rates and a large amount of randomness to the schooling process. Narrow distributions are favored by large exit rates and low randomness in the schooling process. Additionally, wide distributions are favored for schools with a low fish density per cubic meter, and narrow distributions of diameters are favored with high density schools. The density of fish in schools is related to the fish length so the analysis infers that large fish should have a wide probability distribution of large diameters and small fish should develop a narrow probability distribution of small diameters.

From a commercial fishing viewpoint factors that affect school sizes are important and so, briefly, we consider a possible qualitative response of school diameter to fishing activity. If we envision the fishing process as an event that divides a school and removes one of the fractions, then we expect fishing should at least affect the deterministic parameters of the model. The dividing of the school, by fishing, decreases the mean time interval between school divisions and this, in turn, would increase the exit rate coefficient β. The fact that part of the stock is removed by fishing may increase the time interval between school encounters and thus decrease the entrance rate α. A con-

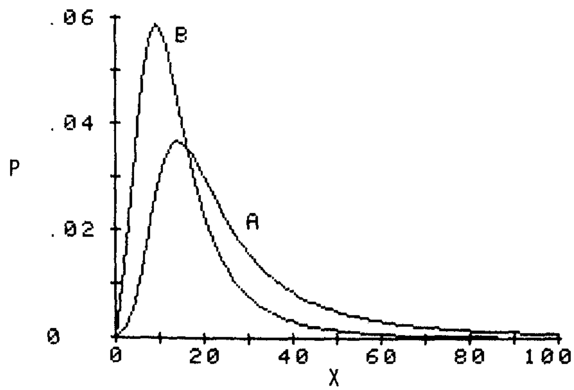

FIGURE 9.—Probability distribution (P) vs. school diameter (X) in meters. Curve A, distribution corresponding to Smith's (1970) observations. Curve B, distribution postulated for fishing activity that increases β and decreases α by 50%.

comitant increase in β and decrease in α would shift the probability distribution towards a narrow range of small diameters. For example, if we assume an increase in fishing activity off southern California decreases α and increases β by 50%, then there would be a noticable decrease in the occurrence of schools >20 m diameter (Figure 9).

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