Reports

Modeling Long-Term Fluctuations in Fish Stocks

Abstract. *Many pelagic fish stocks change rapidly in abundance, with intervening periods of about 50 years. The physical environment does not display such abrupt changes but has a variance that increases with time. A simple population model with multiple equilibrium states exhibited the observed behavior when subjected to this type of stochastic variability. The periodicity exhibited by the model is of the same order as the observations. Thus the assumption by fisheries management of a natural persistence in stocks is questionable.*

Some of the most dramatic population fluctuations occur in pelagic fish stocks (*1, 2*), but there are no obvious or simple general relations to contemporaneous variations in climate or to physical changes in the ocean. Fluctuations in pelagic species such as Pacific sardine or Atlantic herring have occurred about every 50 to 100 years; populations have ranged from high to low with intervening periods when the abundances are relatively constant (*3*). In recent years fish stocks have been affected by heavy fishing and display more frequent but equally large fluctuations. The scientific and management tasks are to separate the natural from the man-made factors contributing to these large and relatively sudden changes. Evidence (*1, 4, 5*) suggests that these alterations affect not only several fish species but also many other components of the food webs in areas such as Georges Bank and the North Sea. One time series of plankton hauls illustrate these observations (Fig. 1, A and B). The implication, assumed here, is that these shifts can be regarded as jumps between alternative equilibrium states of ecological systems.

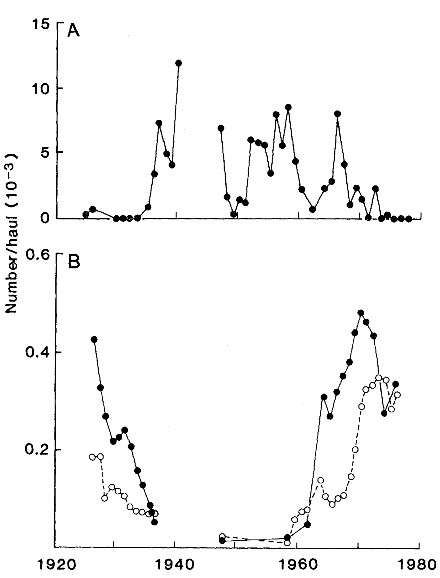

Fig. 1. Changes in fish populations off the coast of Plymouth, England, measured on the basis of weekly plankton samples. (A) Pilchard eggs; (B) postlarval teleosts (excluding clupeids) divided into spring (●) and summer (○) spawners (*5*).

The physical and chemical marine environment varies considerably at all time scales, but excluding the regular daily, lunar, or season cycles the changes are never as pronounced as are the regional biological changes. A particular feature of properties for which we have relatively long records (such as temperature and sea level) (*6*) is that the variance per unit frequency interval increases as the period increases from days to decades. This "red" spectrum (by analogy with red light) is significantly different from the "white" noise, where variance is constant with frequency. Spectra with white noise are used traditionally for stochastic simulations of variability (*7*) and may be appropriate for terrestrial systems (*8*), but they are an inadequate description of marine systems over a wide range of time scales. We have combined a simple ecological model that produces two equilibrium states with red stochastic input to show that the observed time sequences in regional fish stocks can be reproduced.

The ecological model combines the classical logistic growth formula (*9*) with an S-shaped predation function (*10*). These functional relations have been used widely for a variety of ecosystems, such as the spruce budworm and plankton (*11*). The general applicability of the model has been reviewed (*12*).

For a population P,

$$\frac{dP}{dt} = aP(1 - P/b) - cP/(d^2 + P^2) \quad (1)$$

where a represents intrinsic growth rate, b is the carrying capacity, c is a consumption rate dependent on predator population size, and d relates to the catchability of prey P by the predator.

We have normalized the equation by taking $a = d = 1$, so that

$$\frac{dP}{dt} = P(1 - P/b) - cP/(1 + P^2) \quad (2)$$

has only two coefficients (Fig. 2A). Both b and c can be changed by fishing effort as well as by natural environmental fluctuations (*13*). The stochastic variations are introduced by expressing c as a truncated Fourier series:

$$c = c_0 + c_1 \sum_{n=1}^{30} \sin\,[2\pi(tfn + \theta_n)]/n \quad (3)$$

where t is time and f is frequency. The sequence is generated by randomizing θ_n. These fluctuations have a variance proportional to f^{-2}, which is close to observed and theoretical values (*6, 8*).

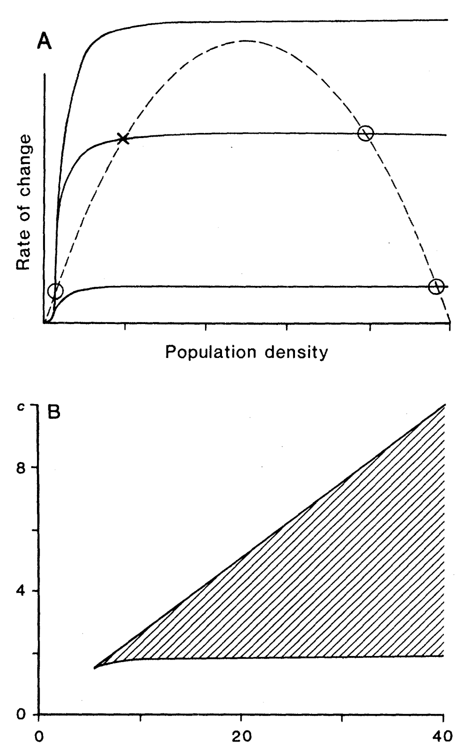

Fig. 2. (A) Rate of change due to growth (- - -) and variable predation (——) showing the different stable (○) and unstable (X) equilibria. Similar relations would be generated by varying growth, a, and keeping constant predation, c. (B) The shaded area defines the region, for varying b and c, where triple-valued solutions of Eq. 2 occur.

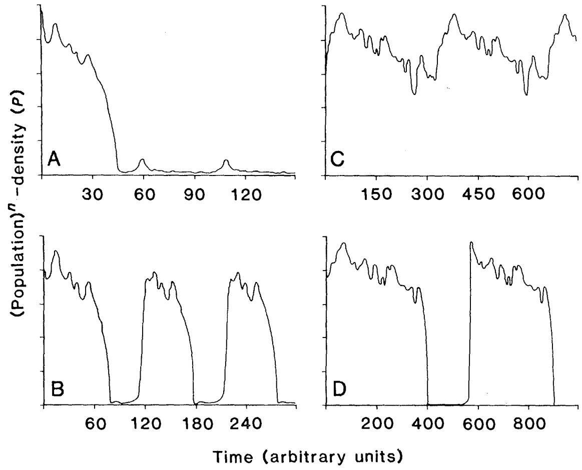

Fig. 3. Computer simulations with (A) $b = 15$ and $f = 0.02$; (B) $b = 15$ and $f = 0.01$; (C) $b = 30$ and $f = 0.003$; and (D) $b = 30$ and $f = 0.002$. Runs were over several cycles to test for system equilibration. Note the changes in time scale between all of the runs.

This simple model in its deterministic form ($c_1 = 0$) generates bifurcations (*12*) as b or c is varied, and the triple-valued region can be expressed as a function of b and c (Fig. 2B). For given b and c, the stable equilibrium state depends solely on the initial value of P. However, when c varies stochastically ($c_1 \neq 0$) over a range of frequencies, a different performance is observed. Values of c_0 and c_1 were chosen so that c would cross upper and lower boundaries (Fig. 2B). The results are not sensitive to the actual values as long as this condition is fulfilled.

Numerical simulations were used to explore the response of the system to variations in b and f. The first conclusion is that, unlike the deterministic case, the response is no longer dependent on initial conditions and responds only to the variability. The second result is that, for any given value of b, the response is dependent on the lowest frequency f in the stochastic input (Fig. 3). There appears to be a narrow range of frequency where the system makes the transition from a single equilibrium state to a two-valued system. A transition frequency, f_c, can be defined as the value of f at which the system reaches 75 percent of the full range between the two values. The value of f_c depends on b, and the relation has two major features (Fig. 4). For larger values of b the value of f_c is nearly constant. Taking the intrinsic response rate of the system as $a = 1$, these values of f_c are small compared to the maximum growth rate of the population. Thus the time between alterations in equilibrium state can be long in relation to the population's own time scales.

As b decreases, possibly because of environmental changes or increases in fishing pressure, the period between these abrupt changes can decrease significantly by a factor of about 6 or 7. Finally, from examination of the cross-spectral relations, there is no simple relation between the variable input, c, and the values of P; this result is in accord with the lack of such relations in field observations.

The results of the simulations (Fig. 3) show that, with low-frequency red noise, the model switches in a way that is qualitatively similar to observation (Fig. 1, A and B). To compare the model results with observations, the arbitrary time scale used in the model must be put in absolute units by determining the rate a, defined as the rate of change of populations at low relative densities.

This is a familiar problem in determining the lower end of the stock/recruitment curve. Such data were obtained during the precipitous decline in North Sea herring stocks, and an a value of about 3 or 4 was obtained from the fitted Ricker curve (*14*). A rapidly growing population, the sand lance (*Ammodytes* spp.) in the New England region, appeared to increase by about one order of magnitude in each of two successive years (*15*); this would correspond to an a value of 2 or 3. A value of $a = 3$ per year would give absolute frequencies of $3f_c$ per year. Thus, for large b in Fig. 3, the critical period would be approximately 100 years, with alterations between equilibrium states occurring at 50-year intervals; this is in good agreement with observations in the historical records. This simple model deals only with one population, P, without age structure, whereas the observations suggest that other large ecosystem changes take place concurrently and that fish stock changes may be confined to critical phases in the larval or juvenile stages of life.

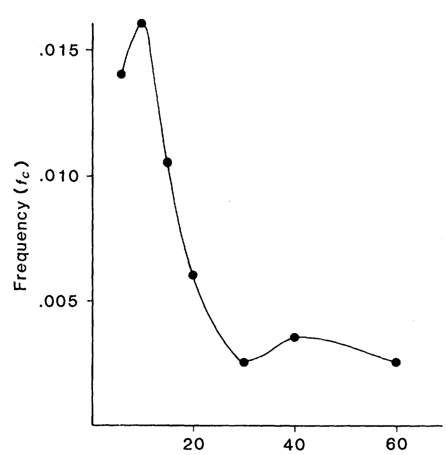

Fig. 4. The relation of b to f_c, the critical value of f at which the system jumps between the two equilibrium states.

In the context of fisheries management, there is usually a tacit assumption that we are operating within periods where stocks are persistent, albeit with large year-to-year fluctuations in recruitment. The data (*5*) (see Fig. 1) suggest that the period 1920 to 1960, when much of fishery theory and practice was developed, was such an interval. More recently, large concurrent changes in stocks cast doubt on this assumption and raise critical management questions about the relative significance of environmental and fishery factors (*15*). The simple model used in this study suggests that the consequences of these two elements can be similar, with small or gradual changes in the environment producing sudden and dramatic consequences. Further, the effects of a decrease in b which can be caused by increased fishing effort (*13*) appear to increase significantly the frequency of these marked changes in abundance. This would imply that the traditional steady-state assumption for management is no longer appropriate and that the rapid succession of dominant species every few years in New England waters and in the North Sea (*16*) may be considered as an acceleration of the longer period, ecological jumps observed in the historical record rather than inadequate control of naturally persistent populations.

JOHN H. STEELE
Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543
ERIC W. HENDERSON
Marine Laboratory, Victoria Road, Aberdeen AB9 8DB, Scotland

References and Notes

1. D. H. Cushing, *Climate and Fisheries* (Academic Press, New York, 1982), p. 373.
2. A. Soutar and J. D. Isaacs, *U.S. Fish. Wildl. Serv. Fish. Bull.* **72**, 257 (1974); F. Devold, *Rapp. P.V. Reun. Cons. Int. Explor. Mer* **154**, 98 (1963). These changes occur in relatively self-contained breeding stocks and are considered distinct from the shorter term, year-to-year changes in distribution or recruitment that can occur with pelagic species and that may be related to interannual fluctuations [D. B. Chelton, P. A. Bernal, J. A. McGowan, *J. Mar. Res.* **40**, 1095 (1982)].
3. Highly variable recruitment is recognized as a

major ecological problem, possibly mediated by short-term weather variations [R. Lasker, *Fish. Res. Bull.* **73**, 453 (1974)]. In under-fished or moderately fished stocks this variability can be partially smoothed at the population level by the existence of a wide range of year classes.
4. B. E. Skud, *Science* **216**, 144 (1982).
5. A. J. Southward, *Nature (London)* **285**, 361 (1980).
6. W. H. Munk and D. E. Cartwright, *Philos. Trans. R. Soc. London* **259** (1966); C. Wunsch, *Evolution of Physical Oceanography* (MIT Press, Cambridge, Mass., 1981), pp. 342–374; J. D. Hays, J. Imbrie, N. J. Shackleton, *Science* **194**, 1121 (1976). There may be a continuous increase in sea-level variance from the instrumental to the geological record bridging the data gap between decades and millenia (J. Imbrie, personal communication). The general relation is of the form-variance per unit frequency α [(frequency)$^{-n}$], where $1.5 < n < 2$.
7. White noise was used to investigate the response time of a logistic fishery model to stochastic variation [J. R. Beddington and R. M. May, *Science* **197**, 463 (1977)].
8. Reviews of atmospheric and tree ring data [U.S. Committee for the Global Atmospheric Research Program, *Understanding Climatic Change: A Program for Action* (National Academy of Sciences, Washington, D.C., 1975), p. 239] show spectra that are white to frequencies of about 0.01 (100-year periods). Simple stochastic models of atmosphere-ocean physical interactions have been shown to transform white noise to red noise in the ocean [P. Lemke, *Tellus* **29**, 385 (1977)].
9. E. C. Pielou, *An Introduction to Mathematical Ecology* (Wiley, New York, 1969).
10. C. S. Holling, *Mem. Entomol. Soc. Can.* **45**, 60 (1965).
11. D. Ludwig, D. Jones, C. Holling, *J. Anim. Ecol.* **47**, 315 (1978); J. H. Steele and E. W. Henderson, *Am. Nat.* **117**, 676 (1981).
12. R. May, *Nature (London)* **269**, 471 (1977).
13. The effect of fishing effort, E, on the population, P, is conventionally represented by an additional term, $-EP$. This is included in the logistic function and results in a decrease in a and b. Some types of fishing effort may also be expressed through the predation term c [O. Ulltang, *Rapp. P.V. Reun. Cons. Int. Explor. Mer* **177**, 489 (1980)].
14. A. Saville and R. S. Bailey, *ibid.*, p. 112.
15. K. Sherman, C. Jones, L. Sullivan, W. Smith, P. Berrien, L. Ejsymont, *Nature (London)* **291**, 486 (1981).
16. J. W. Horwood, *Dynamics of Large Mammal Populations* (Wiley, New York, 1981), p. 339.

28 November 1983; accepted 26 March 1984

The Vega Particulate Shell: Comets or Asteroids?

Abstract. *The Infrared Astronomical Satellite (IRAS) science team has discovered a shell of particulate material around the star Vega. At the mean distance and temperature of the shell, the expected condensation products from a protostellar nebula would be dominated by frozen volatiles, in particular water ice. It is not possible to discriminate between dirty ice and silicate materials in the Vega shell on the basis of the IRAS data. The Vega shell is probably a ring of cometary bodies with an estimated minimum mass of 15 earth masses, analogous to one that has been hypothesized for the solar system. A possible hot inner shell around Vega may be an asteroid-like belt of material a few astronomical units from the star.*

The Infrared Astronomical Satellite (IRAS) science team (*1*) has reported the discovery of a shell of particulate material around the star Vega, α Lyr. The shell has an apparent diameter of 20″, corresponding to a distance from Vega of 85 AU, and its infrared spectrum can be fitted by a blackbody curve with a temperature of 85 K. The observations have been interpreted by the IRAS team as indicating a shell of particulate material with particle diameters on the order of 0.12 cm or more and with a possible mass between 1.2×10^{-2} and 300 earth masses. The existence of the Vega shell has been confirmed by observations at 47 and 95 μm with the Kuiper Airborne Observatory (*2*). Similar shells of material have also been found around the star Fomalhaut, α PsA, and two other stars (*3*).

In our own solar system a shell with a temperature of 85 K would correspond to a location about 10 AU from the sun, roughly the semimajor axis of Saturn's orbit. The small bodies that condensed from the primordial solar nebula at that distance are predominantly water ice, for example, the icy satellites of Saturn. Kuiper has suggested (*4*) that comets, which are primarily water ice, formed among the outer planets prior to being ejected to the sun's Oort cloud.

It is therefore reasonable to ask whether the material around Vega is of cometary or asteroidal origin. If the condensation processes in the proto-Vega nebula were similar to those in the solar nebula, and there is no reason to expect that they were not, then the dominant condensate 85 AU from Vega would be water ice. Ice and dust grains in the proto-Vega nebula would settle toward the nebula midplane, where they would form an accretion disk and then break up and contract into cometesimals through Goldreich-Ward gravitational instabilities (*5*). The Goldreich-Ward theory predicts cometesimals (in our solar system) with typical diameters of 100 to 300 km, although a more recent study (*6*) has shown that accelerated settling of larger dust and ice grains would lead to bodies of more modest size, typically 8 km in diameter, in agreement with estimates for the dimensions of observed cometary nuclei (*7*).

Because of the long orbital period at 85 AU from Vega, 554 years, growth of significantly larger bodies through collisional accretion of the initial cometesimal population would probably not have occurred in the 10^8-year estimated lifetime of Vega. At the expected temperature 85 AU from Vega, water ice bodies would be stable against sublimation over the lifetime of the Vega system. Water ice sublimation rates are fairly negligible at temperatures below about 160 to 170 K (*8*).

Moreover, it is not possible to discriminate between dirty water ice and silicate particles on the basis of the IRAS data. The addition of relatively small amounts of absorbing material to water ice particles sharply reduces their albedo and leads to thermal behavior approaching that of a blackbody as a function of solar distance (*9*). For nonsublimating, fast-rotating particles in orbit about Vega (and if we ignore thermal conduction terms), the mean temperature (in kelvin) is given by

$$T = 767[(1 - A)/r^2]^{1/4} \qquad (1)$$

where A is the particles' albedo and r is the distance from Vega (in astronomical units). For a blackbody at 85 AU, Eq. 1 predicts $T = 83.2$ K. For a typical S-type asteroid with $A = 0.15$, T drops to 79.9 K; for a cometary nucleus covered with a bright snow with $A = 0.4$, T is 73.2 K. But, if the snow is dirtied with even small amounts of dark material, A decreases sharply and T increases to close to that for a blackbody. The addition of only 10 percent (by weight) silicate soil to water ice can lower A from 0.48 to 0.14 (*10*); contamination with 10 percent carbon would lower A to 0.10. Typical ratios of dust to ice in comets are estimated to be between 0.5 and 2.0 (*11*).

In addition, if the particles producing the infrared emission from the Vega shell are on the order of several micrometers in size or smaller, then their effective temperature can in fact exceed the blackbody temperature for their distance from Vega. This results from the inefficiency with which micrometer and submicrometer particles radiate energy at thermal wavelengths.

The IRAS science team (*1*) set a lower limit on the diameter of particles in the Vega shell of 0.06 cm, arguing that particles up to 9 μm in diameter would be blown away by radiation pressure and that particles smaller than 0.06 cm would have spiraled into Vega as a result of the Poynting-Robertson effect. However, neither of these arguments need apply if the particles are being continually supplied by sublimation from and collisions between larger bodies orbiting in the shell. Because of the low temperature of the Vega shell, water-ice sublimation would be negligible and a more volatile ice such as methane ice would be re-