

## **Randomness, Synchrony and Population Persistence**

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The dynamics of populations whose life cycle includes a stage which is resistant to the external disturbances, is examined over a large range of time scales of the environmental change. Using non-Markovian models it is shown that when the disturbance and the resistant stage have comparable time scales, population persistence increases with increasing duration of disturbance; persistence in all harshly varying environments depends on the level of synchronization of the environmental and population processes. Results also show that population dynamics in fully periodic environments cannot approximate the dynamics in stochastic environments, and it is suggested that increasing number of sources of variation in the environment accounts for increasing stability of population trajectories. Applications to empirical studies of population dynamics and life history strategies, as well as to parasite and pest control problems, are briefly discussed. It is conjectured that drugs and pesticides may be more effective when applied at variable intervals.

### **1. Introduction**

The need for synchronizing biological activity with the time in which the environment is most suitable for that particular activity is quite obvious. Indeed many striking examples are known of subordination of plants and animals, by means of their physiological clock, to the diurnal and lunar cycles (Bünning, 1964).

When environmental variation includes episodes of total non-production and death, the ability to escape these detrimental effects by means of a resistant life stage can be of prime importance. In such regimes the realized population growth may well depend more on the synchrony of the resistant life stage with the period of devastation, and less on deterministic population properties such as the intrinsic growth rate, interaction coefficients etc.

In areas where harsh periods, in the form of cold winters, droughts etc., are seasonal events, a period of resistance (e.g. dormancy) fully synchronized with the solar cycle presumably evolves in a straightforward manner. But natural systems are often subject to unpredictable periods of devastation: occasional rainless winter months can cause extinction of most newly

germinated seedlings of annual plants in the desert (Ellner & Shmida, 1981), the shearing force of storm waves removes patches of mussels from their base (Paine, 1978), and occasional catastrophic low tides, lasting several days can cause as much as 90% mortality of hermatypic corals on the reef flat (Loya, 1976). Human intervention is another source of unpredictable disasters for nature, taking the form of long lasting effects of pollution on coral reefs (Loya & Rinkevich, 1980) or of pesticides, heavily applied at variable intervals. It seems obvious that as in the case of seasonal environments, persistence in unpredictable environments should also depend on the synchrony between the period of resistance and the period of disturbance. However, where the variations are not regularly periodic synchronization becomes a more complicated problem.

Whereas existing stochastic models assume that the time scale of the environmental change is much smaller than that of the population change, the examples given show that environmental noise can often be on the same time scale as the biological period. The model presented in this article is new in allowing for this property. It concerns organisms whose life cycle consists of a non-reproducing stage that is immune to the environmental disturbance. The duration of disturbance varies from a time scale much

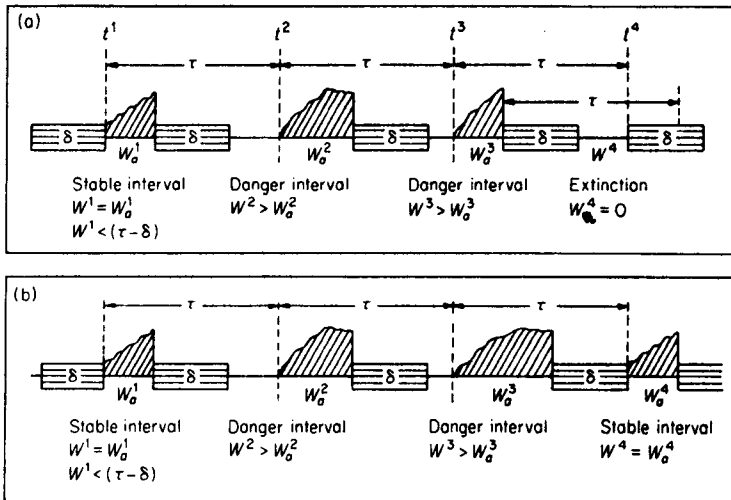


FIG. 1. The dynamics of the system in the region  $1 < \tau/\delta \leq 2$ . ■ A period of disturbance—all adults die. — A favourable period with no adults in the system. ▨ Adults present in the system. (a) The process leading to extinction. The stable interval of duration,  $W^1 < (\tau - \delta)$ , initiates a sequence of danger intervals. Extinction occurs in the  $n$ th interval,  $W_a^n = 0$ , when  $W_a^{n-1} + W^n \leq (\tau - \delta)$ . (b) The system returns to a "stable state" in the  $n$ th interval,  $W^n = W_a^n$ , when  $W_a^{n-1} \geq (\tau - \delta)$ .

shorter than the resistant stage to one of the same order as that of the resistant stage. Analysis of the model shows that the sequence of events that bring about extinction depends on the relative time scales.

When only one disturbance can be incorporated in a life time of the resistant stage, every harsh period is bridged by juveniles born in the previous interval only. This renders a Markovian-like property to such systems and, hence, the model can be analysed for all distributions of intervals between disturbances, by the application of elementary methods. Results show that the average extinction time may actually increase with increasing duration of disturbance!

When recruitment in an interval can be accomplished by juveniles born in several preceding intervals, the number of states of the system becomes intractably complicated, and a general solution can no longer be obtained. Nevertheless, by assuming specific distributions of the favourable periods, one can gain insight concerning the nature of the synchrony between the biological and the environmental processes.

The third part of the paper describes simulation results of a model consisting of a differential equation assumed to describe the intrinsic population growth. These results are compared with the analytic results and biological implications are discussed.

## 2. The General Model

Consider a population which has two life stages: a juvenile stage of length  $\tau$ , resistant to the environmental disturbance, and an adult, susceptible, stage which produces juveniles continuously (see Fig. 1 and Table 1). The environment is characterized by alternating harsh and favourable periods. Harsh periods take the form of disturbances that completely obliterate all adults including the juveniles that are recruited (i.e. that become adult) during the period  $\delta$ , in which a disturbance prevails. The duration of the intervals between disturbances, i.e. the favourable periods, is assumed to

TABLE 1  
*Parameters and variables in the basic model*

$\tau$	the duration of the juvenile stage, which in this model defines the biological period
$\delta$	the duration of the environmental disturbance
$\varphi$	the frequency of disturbance, so that $\bar{W} = 1/\varphi$ is the average interval between the end of one disturbance and the beginning of the next one
$W^i$	the duration of the interval $i$ between two subsequent disturbances
$W_a^i$	the episode of adults in the interval $i$
$t^i$	the initiation time of adult recruitment in the interval $i$

be strictly positive. The deterministic rate of increase is taken as high enough to guarantee that as long as there is recruitment in an interval between disturbances some adults will prevail to the end of that interval. Other details of the deterministic population dynamics are ignored.

Recruitment in any given interval between disturbances can be made by juveniles born during any of one or more preceding intervals, depending on the relation between the biological and environmental periods. The relative time scale,  $N$ , of a given system is defined here as the maximal number of environmental periods that can be incorporated in a single biological period. It is shown hereafter that this definition plays an essential role in the analysis of extinction patterns.

(A) DISTURBANCES AND RESISTANT FORM HAVING COMPARABLE TIME SCALES

This section is intended to describe the pattern of extinction when disturbance and resistant stages are of comparable duration and to prove that in such systems the time to extinction increases with increasing duration of disturbance.

In the region

$$1 < \tau/\delta \leq 2 \quad (1)$$

$N = 1$ , for all distributions of intervals. When  $\tau$  and  $\delta$  obey equation (1) and as long as the intervals are large enough, the initiation of adult recruitment in an interval,  $i$ , denoted by  $t^i$ , coincides with the initiation of that interval. Once there occurs an interval whose duration,  $W^i$ , obeys

$$W^i < (\tau - \delta)$$

then the initiation of recruitment in all subsequent intervals will have a fixed period,  $\tau$ , with the position of the epoch  $t^{i+1}$ ,  $t^{i+2}$ , ... varying within intervals (Fig. 1). Population is extinct upon the occurrence of an interval, the  $n$ th, say, which is too short to include the epoch  $t^n$ , so that recruitment is fully overlapped by the following disturbance. The state of the population in any interval belongs, therefore, to one of three categories:

1. A stable state, when the epoch  $t^i$  coincides with the initiation of the interval,  $i$ , so that the period of adults,  $W_a^i$  that commences with  $t^i$  and terminates with the beginning of the next disturbance obeys

$$W_a^i = W^i.$$

2. A danger state, when the epoch  $t^i$  falls within the interval  $i$ , so that

$$W_a^i < W^i.$$

3. Extinction, when the epoch  $t^i$  coincides with the occurrence of a disturbance, so that

$$W_a^i = 0.$$

The interrelationships between these three states is sketched in Fig. 2.

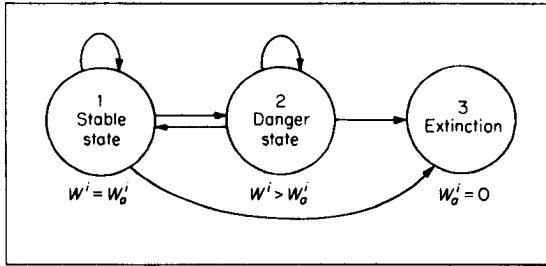


FIG. 2. The state chart of population dynamics, determined by the episodes of adults within the favourable periods. The trajectory leading from a stable state to extinction, directly or through the intermediate, danger state, is described by equation (5b). The trajectory from a stable state to a danger state and back to a stable state is described by equation (6).

The process of extinction may be described, then, through the periods of adults in the chain of intervals.

Let  $W^1$  be an interval in a stable state so that

$$W^1 = W_a^1 \tag{2a}$$

$$W^1 < (\tau - \delta). \tag{2b}$$

From equation (1) it is then clear that the following interval is in a danger state,  $W_a^2 < W^2$  (see Fig. 1(a)).  $W^2$  and all subsequent intervals are danger intervals as long as each one of them contains a period of adults satisfying

$$(\tau - \delta) \geq W_a^i > 0$$

$$W_a^n = 0 \quad \text{if } W^n \leq (\tau - \delta) - W_a^{n-1} \tag{3}$$

$$W_a^{n-1} = W^{n-1} - (\tau - \delta) + W_a^{n-2}$$

and from this recursion and equation (2(a)) we set

$$W_a^{n-1} = \sum_{i=1}^{n-1} W^i - (n-2)(\tau - \delta). \tag{4}$$

Thus the conditions for extinction in the  $n$ th interval are

$$W^1 = W_a^1; \quad W^1 < (\tau - \delta) \tag{5a}$$

$$\sum_{i=1}^n W^i \leq (n-1)(\tau - \delta). \tag{5b}$$

If  $W_a^n \geq (\tau - \delta)$ , then the next interval will be stable (Fig. 1(b)), that is:

$$\text{if } W_a^n \geq (\tau - \delta), \text{ then } W_a^{n+1} = W^{n+1}.$$

$$\text{Now } W_a^n \geq (\tau - \delta) \text{ if } W^n \geq 2(\tau - \delta) - W_a^{n-1}$$

and from equation (4) it is clear that the conditions for returning to a stable state in the interval  $n + 1$  are

$$\begin{aligned} W^1 &= W_a^1; \quad W^1 < (\tau - \delta) \\ \sum_{i=1}^n W^i &\geq n(\tau - \delta). \end{aligned} \quad (6)$$

The population will still be in a danger state in the  $n$ th interval, if:

$$n(\tau - \delta) > \sum_{i=1}^n W^i > (n-1)(\tau - \delta). \quad (7)$$

From equations (5b) and (6) it is evident that for a given distribution of intervals, extinction will occur earlier, both in calendar time and in the count of intervals (the period index), the larger are the values of  $\tau - \delta$ . Return to a stable state will occur earlier for smaller values of  $\tau - \delta$ . This conclusion can be restated in the following manner.

*Corollary 1.* For any distribution of the process ( $W^1, W^2, W^3, \dots$ ), the extinction time and the extinction period index in environment  $B$  are stochastically larger than those in environment  $A$ , when

$$\tau/2 \leq \delta_A < \delta_B < \tau.$$

*Corollary 2.* For any distribution of the process ( $W^1, W^2, W^3, \dots$ ), the extinction period index of population  $B$  are stochastically larger than those of population  $A$ , when

$$\tau_A/2 \leq \delta < \tau_B < \tau_A.$$

Maximum synchronization of the population with the stochastic environmental process is achieved when

$$\tau/\delta \rightarrow 1^+.$$

#### (B) DISTURBANCES OF A RELATIVELY SMALL TIME SCALE

The dependence of the average time to extinction (to be denoted AET) on the frequency of disturbance, will be analysed for  $N=2$ . Extinction occurs here in the interval  $n$ , given

$$W_a^{n-2} > 0$$

if

$$W_a^{n-1} = 0 \quad \text{and} \quad W_a^n = 0. \quad (8)$$

The probability of equation (8) depends on the state of the interval  $n-3$ . Given  $W_a^{n-3} > 0$ , the conditions for equation (8) are defined as follows:

$$W_a^{n-3} + W^{n-2} + W^{n-1} \leq \tau - 2\delta \tag{9}$$

and

$$W_a^{n-2} + W^{n-1} + W^n \leq \tau - 2\delta \tag{10}$$

(Fig. 3(a))

or

$$W^{n-2} \geq \tau - 2\delta \tag{11}$$

and

$$W^{n-1} \geq \tau - 2\delta \tag{12}$$

and

$$W_a^{n-2} + W^{n-1} \leq \tau - \delta \tag{13}$$

(Fig. 3(b))

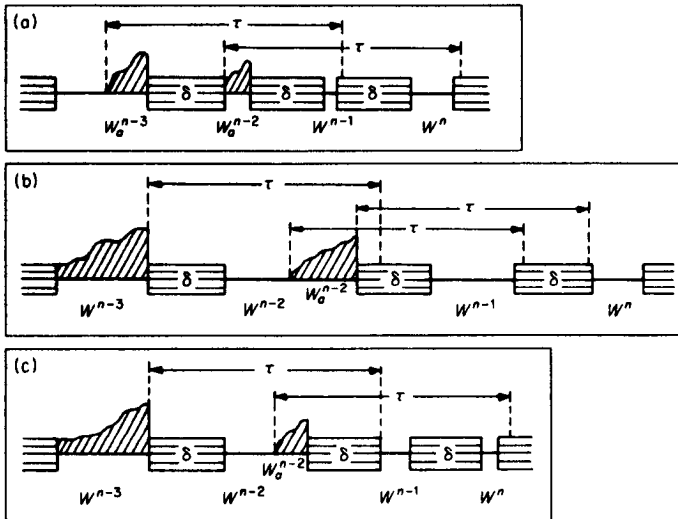


FIG. 3. The three sequences of extinction in the region  $2 < \tau/\delta \leq 3$ . (a) When the frequency of disturbance is large, extinction most probably occurs if:  $W_a^{n-3} + W_a^{n-2} + W^{n-1} \leq \tau - 2\delta$ ; and  $W_a^{n-2} + W^{n-1} + W^n \leq \tau - 2\delta$ . (b) When the frequency of disturbance is small, extinction most probably occurs if  $W^{n-2} \geq \tau - 2\delta$ ; and  $W^{n-1} \geq \tau - 2\delta$ ; and  $W_a^{n-2} + W^{n-1} \leq \tau - \delta$ . (c) Extinction can also occur if  $W_a^{n-2} + W^{n-1} + W^n \leq \tau - 2\delta$ ; and  $W^{n-2} \geq \tau - 2\delta$ .

or

$$W_a^{n-2} + W^{n-1} + W^n \leq \tau - 2\delta$$

and

$$W^{n-2} \geq \tau - 2\delta$$

(Fig. 3(c))

The conditions for extinction when  $W_a^{n-3} = 0$ , are easy to define. Doing so it becomes evident that the probability of extinction is always higher for  $W_a^{n-3} > 0$ . Moreover, when the frequency of disturbance is very large, extinction will most probably occur through the combination of events (9) and (10). Note that (9) and (10) can be generalized for all relative time scales: for all  $N$  and large frequency of disturbance, the condition for  $W_a^n = 0$  is given by

$$W_a^{n-N} + \sum_{i=n-N+1}^n W^i \leq \tau - N\delta. \quad (15)$$

When disturbance frequency is small extinction will most probably occur through the sequence (11) and (12) and (13).

It appears then that when the relative time scale is higher than unity, it is the frequency of disturbance that governs the pattern of change of the AET as a function of the relation  $\tau/\delta$ . As for  $N=1$ , here too, extinction results from a combination of events in which short intervals give rise to short episodes of recruitment that are fully overlapped by disturbance. When the frequency of disturbance is very large then a dense group of  $N$  disturbances has the same effect as one disturbance of duration  $N\delta$ . Such systems will show the same result as before, namely that the time to extinction for each relative time scale increases with increasing duration of disturbance. When the frequency of disturbance is small the results are in accord with the common sense: the probability of a short episode of recruitment being overlapped by a disturbance is positively related to  $\delta$ , so that the time to extinction decreases with increasing duration of disturbance.

### 3. Specific Environments

#### (A) EXPONENTIAL DISTRIBUTION OF INTERVALS

Let us assume that the distribution of intervals between disturbances is exponential. As intervals, assumed in this model to be strictly positive, can still be infinitesimally small, the relative time scale as defined above, is



determined by the ratio,  $\tau/\delta$ , as follows

$$1 < \tau/\delta \leq 2, \text{ for } N = 1.$$

$$2 < \tau/\delta \leq 3, \text{ for } N = 2.$$

When  $N = 1$ , we see from equation (3) that the condition for having no recruitment in the interval  $n$  is

$$W_a^{n-1} + W^n \leq \tau - \delta.$$

In order to estimate the probability of this event and the average extinction time, we use a property of the exponential distribution which can be phrased as follows: if the intervals between disturbances,  $W^i$ , are mutually independent with a common exponential distribution and recruitment in an interval,  $i$ , begins in an epoch  $t^i$  which is not dependent on the limits of  $i$ , then the period of adults in  $i$ ,  $W_a^i$ , has the same exponential distribution as  $W^i$ .

The probability of equation (3),  $p_1$ , will be

$$p_1 = 1 - \exp[-\varphi(\tau - \delta)][1 + \varphi(\tau - \delta)] \tag{16}$$

where  $\varphi$  is the average frequency of disturbance.

The average time to extinction measured by the period index,  $\bar{n}$ , is defined by

$$\bar{n} = \sum_{k=1}^{\infty} k p_1 q^{k-1} = p_1^{-1} = \{1 - \exp[-\varphi(\tau - \delta)][1 + \varphi(\tau - \delta)]\}^{-1} \tag{17}$$

where  $q = 1 - p_1$ .

The average time to extinction in calendar time,  $\bar{T}$ , is given by

$$\bar{T} = \bar{n}\tau. \tag{18}$$

As the derivative of  $p_1$  with respect to  $\delta$  is negative we conclude that the AET always increases for  $\delta$  varying from  $\tau/2$  to  $\tau$ .

For all  $N$ , and exponential distribution of intervals, the probability of the sequence (15),  $p_2$ , will be

$$p_2 = 1 - \exp[-\varphi(\tau - N\delta)] \sum_{i=0}^N [\varphi(\tau - N\delta)]^i / i!. \tag{19}$$

Numerical calculation of equation (19) shows that  $p_2$  increases when  $\tau/\delta$  varies from 2 to 3 ( $N = 2$ ), from 3 to 4 ( $N = 3$ ), . . . .

It is argued above that when  $\varphi$  is small, extinction for  $N = 2$  occurs most probably through the sequence (11) and (12) and (13). The probability of this sequence,  $p_3$ , is given by

$$p_3 = \int_{y=\tau-2\delta}^{\tau-\delta} \int_{x=\tau-2\delta}^{\infty} \frac{\tau - \delta - y}{x} \varphi^2 \exp(-\varphi x) \exp(-\varphi y) dx dy. \tag{20}$$

The derivative of  $p_3$  with respect of  $\delta$  is positive, thus we conclude that for given  $\varphi$  and  $\tau$ ,  $p_3$  decreases when  $\tau/\delta$  varies from 2 to 3.

It is expected then that when  $N = 2$ , increasing frequency of disturbance will cause a change in the location of the maximum in the AET curve, from  $\tau/\delta = 3$  to  $\tau/\delta = 2 + \varepsilon$  ( $\varepsilon$  being small).

#### (B) FULLY PERIODIC ENVIRONMENTS

Assume that the intervals between disturbances have a constant duration,  $W$ . The condition for extinction occurring in finite time is defined by

$$N(W + \delta) < \tau \leq NW + (N + 1)\delta \quad (21)$$

when  $N$  is defined as above. Note that whereas in stochastic environments  $N$  is determined by two parameters, namely  $\tau$  and  $\delta$ , in fully periodic environments  $N$  is determined by three parameters,  $\tau$ ,  $\delta$  and  $W$ . The condition for extinction in the interval  $n$ , starting with  $W^1 = W_a^1$ , when  $\tau/\delta$  lies in the region defined by equation (21) is

$$nW \leq \frac{n-1}{N}(\tau - N\delta). \quad (22)$$

It is clear from equation (22) that for given  $W$ ,  $\tau$  and  $N$ , the time to extinction, when finite, always increases with increasing  $\delta$ . Note that equation (22) reduces to equation (5b) for  $N = 1$ .

#### 4. Simulation Results

In this section population dynamics is treated in a more conventional manner. A logistic type equation is introduced, which describes a particular case of a deterministic population growth. This equation is not a special case of the model described above. Rather, unlike the basic model, here the deterministic growth is limited by the initial conditions and by the intrinsic rate of increase. Comparing results of the two models, one can estimate the contribution of the deterministic elements to the overall population dynamics in harshly varying environments. An external disturbance of the type described above is superimposed on the deterministic equation. It is useful to cast the resulting dynamics of the system in the form of equation (23).

$$x'(t + \Delta t) = \{x'(t) + \lambda'x'(t - \tau)[1 - x'(t)] - \mu x'(t)\}[1 - D(t)] \Delta t. \quad (23)$$

Here  $x(t)$  stands for the number of adults at time,  $t$ ;  $x'(t) = x(t)/K$ , where  $K$  is the carrying capacity of the environment.  $\lambda'$  stands for the reproduction

rate, containing an element of juvenile mortality, so that  $\lambda' = \lambda \exp(-\mu'\tau)$  where  $\lambda$  is the birth rate,  $\mu'$  is the mortality rate of juveniles whose life-span is  $\tau$ .  $\mu$  stands for the mortality rate of adults, and  $D$  is the environmental process, assuming the values 0 and 1. In this model the disturbances have a fixed duration,  $\delta$ . The intervals between disturbances are assumed to be strictly positive, with their duration either exponentially distributed or fixed. For full details of this model see Agur & Deneubourg (1985).

Figures 4, 5 and 6 show simulation results of equation (23) when intervals between disturbances are exponentially distributed. Figure 7 shows results for fixed duration of intervals. In all simulation experiments the initial population size was taken as large enough to avoid any effect on the process of extinction.

Simulation results confirm all the predictions reached above: for all examined disturbance frequencies the AET increases for  $\tau/\delta$  varying from 2 to 1 (Figs 4, 6); for all relative time scales,  $N$ , and large frequencies of disturbance, the AET increases for  $\tau/\delta$  varying from  $N+1$  to  $N$  (Fig. 4); for  $N=2$ , the maximum in the AET curve moves from  $\tau/\delta=3$  to  $\tau/\delta=2+\epsilon$ , with increasing frequency of disturbance (Fig. 5); for  $N>1$ , and small frequencies of disturbance, the AET increases with increasing  $\tau/\delta$  (Fig. 6).

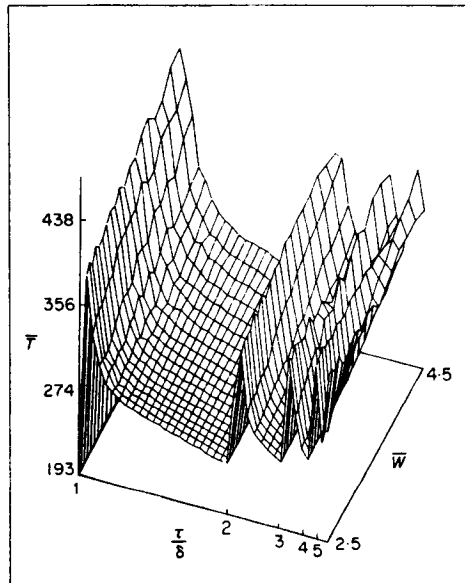


FIG. 4. Simulation results of equation (23). The average time to extinction is plotted as a function of the duration of disturbance. Intervals between disturbances,  $\bar{W}$ , are exponentially distributed.  $N=1, 5$ ;  $\bar{W}=2.5, 4.5$ ;  $\lambda=0.5$ ;  $\mu'=0.01$ ;  $\mu=0.01$ ;  $K=100$ .

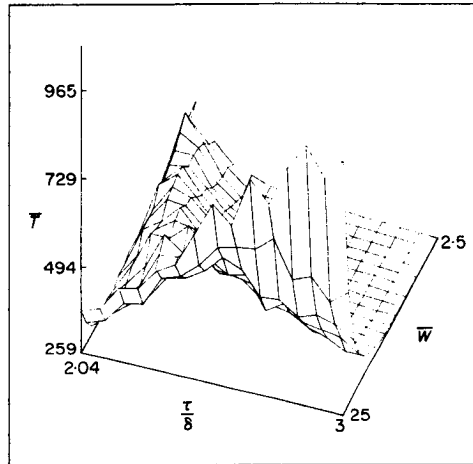


FIG. 5. As in Fig. 4 for  $N=2$ ;  $\bar{W}=2.5-25$ ;  $\lambda=1$ .

Moreover, when  $\varphi$  is relatively large (Fig. 4) a point of discontinuity in the AET curve is observed on  $\tau/\delta = N + \varepsilon$  ( $\varepsilon$  being infinitesimally small). This point marks the switch from minimum to maximum in this curve upon the passage to a higher relative time scale. In Fig. 4 we also notice that the AET decreases for  $\tau/\delta \leq 1.02$ . The reason for this result, which contrasts with corollary 1, lies in the above mentioned difference between the general model and equation (23). Further simulation results (Agur & Deneubourg, 1985), indicate that when a Gaussian distribution in  $\tau$  or in  $\delta$  is allowed for, the points of discontinuity disappear. Still results remain qualitatively unchanged when variance in  $\tau/\delta$  is not too large. Deterministic growth rate affect the pattern of dependence of the AET on  $\tau/\delta$  only when relatively small. Increased patchiness of the habitat is shown to have little effect on this pattern.

The model whose results are displayed in Fig. 6 assumes exponential distribution of intervals between disturbances, while the one simulated in Fig. 7 assumes constant duration of intervals. Thus, whereas environments in Fig. 7 have one source of variation—in the mortality of adults, the environments in Fig. 6 have two sources of variation—varying mortality of adults and varying duration of the favourable period. The system in Fig. 7 appears to be very unstable, in the sense that populations which have been fully synchronized before are driven to extinction by small perturbations in  $\varphi$  or in  $\delta$ , when  $N > 1$ , and when the frequency of disturbance is large. Increasing uncertainty, through the introduction of variation in the duration of the favourable period, increases the stability of the system: the AET is

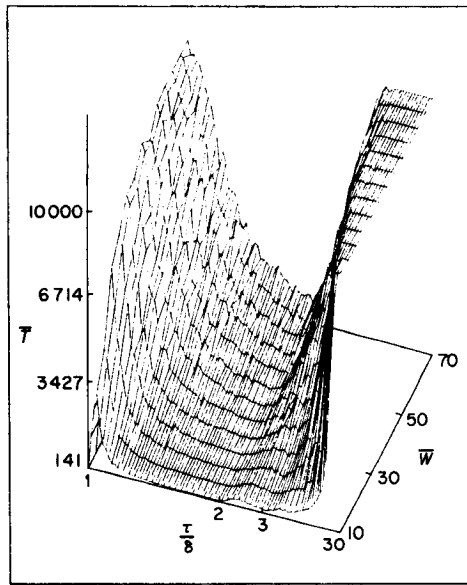


FIG. 6. As in Fig. 4 for  $N = 1, 30$ .  $\bar{W} = 10, 70$ ;  $\lambda = 1$ .

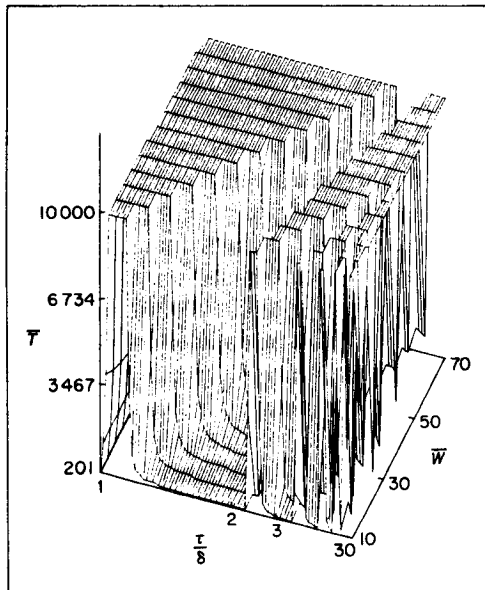


FIG. 7. As in Fig. 6, but intervals between disturbances have now a constant duration,  $W$ .

homogeneously short for most of the studied domain and is maximized for  $\tau/\delta \gg 2$ .

### 5. Conclusions and applications

A meaningful study of population dynamics in harshly varying environments should focus on the characters that determine the capacity for responding to effective hazards. Deterministic growth parameters (such as the intrinsic rate of increase or competition coefficients) are tedious to estimate, and may in appropriate circumstances have only a minor relation to this capacity. The parameter  $r$  for example, amalgamates various intrinsic population parameters, one of which is the duration of the juvenile stage. When this stage is resistant to the environmental disturbance, populations with different juvenile longevities may vary in their ability to buffer disturbances inflicted on adults. This important difference may be concealed in  $r$ , where the contribution of the juvenile stage, in the form of a time delay in reproduction, may be averaged out by the contribution of other parameters.

The results of the present study indicate that population dynamics in varying environments should be classified according to the relative time scale of the biological and environmental processes. This criterion is defined here as the maximal number of environmental periods in a single biological period. In environments that are fully periodic the relative time scale depends on the biological period,  $\tau$ , on the period of the disturbance,  $\delta$ , and that of the favourable interlude between disturbances. In stochastic environments the favourable interludes can be infinitesimally small so that the relative time scale is determined by  $\tau$  and  $\delta$  alone.

When the population and the environmental processes are of the same time scale ( $1 \leq \tau/\delta \leq 2$ ), the time to extinction of a given population can paradoxically increase with increasing duration of disturbance. The time to extinction is maximized when the duration of disturbance is just slightly smaller than the life span of the resistant stage. These results are general for all distributions of intervals between disturbances.

The same counterintuitive result is repeated for higher relative time scales, when the frequency of disturbance is large. That is to say that for each relative time scale the time to extinction increases with increasing duration of disturbance. The opposite result is obtained for relative time scales larger than one, for small frequencies of disturbance and exponential distribution of the intervals. Now the time to extinction of a given population is larger for smaller disturbances.

Theoretically, these patterns should remain qualitatively unchanged in restricted environments, when the intrinsic rate of increase is relatively

large, and when the variances in the juvenile life span and in the duration of disturbance are relatively small.

The evaluation of the ratio  $\tau/\delta$  will often be reasonably straightforward. The relative time scale is given by the integer part of this ratio, while the fractional part measures the level of synchronization within the relative time scale. Rough estimates of the frequency of disturbance and of the variance in  $\tau/\delta$  indicate the extent to which the population trajectory is affected by the level of synchronization with the environmental period.

Polymorphism in the duration of the non-reproducing life-stage is a common phenomenon in plants (Martins & Jain, 1979; Ellner & Shmida, 1981), and animals (Brown, 1978). The advantage of such a polymorphism is usually understood to be in averaging recruitment chances over time, or in altruistically reducing competition among siblings (Ellner & Shmida, 1981). When the different morphs vary in their dispersal range (Ellner & Shmida, MS; Venable & Lawlor, 1980), polymorphism is also assumed to average recruitment over space (Levin, Cohen & Hastings, 1981), or to reduce competition in general (Hamilton & May, 1977), as opposed to the above mentioned group selection mechanism suggested by Ellner & Shmida. The present study implies that disturbed environments encourage dimorphism and polymorphism of the juvenile life-span, when disturbance frequencies are small and large, respectively. This idea differs from the "spreading of risk" notion (Cohen, 1966), in that in our model the polymorphism, *per se*, is not necessarily advantageous. Rather, each of the morphs can be equally persistent on its own, and their common occurrence may be due to ancestral bifurcation. Thus, the same explanation may embrace also cases of monomorphic juvenile longevities that vary greatly among sibling sympatric species, such as the periodical cicadas (Simon, 1983), and intertidal snails (Ayal & Safriel, 1982).

Stability indicators in stochastic environments have been thoroughly discussed by May (1973), Feldman & Roughgarden (1975), Turelli (1978), Yodzis (1978), and Chesson (1982). As was noted by Harte (1979), the shortcoming of much of the theoretical work is that the results are often not expressible as relations among readily measurable quantities. On the other hand, for many practical purposes the impact of environmental variation is most usefully quantified by the average persistence time of the population (Ludwig, 1975). Hence it seems straightforward to measure the stability of systems by the sensitivity of the persistence time to small perturbations of the parameters; a given system can be defined as unstable if a small perturbation in the parameters causes a large change in the average persistence time of the population.

The results presented here imply that the stability of the population trajectory as defined here above, increases with increasing number of sources of variation in the environment: over a large domain of environmental parameters, the persistence time in the periodic system strongly fluctuates, being either infinite or close to zero; the same domain of parameters in the stochastic system gives rise to homogeneously short persistence times.

These conclusions bear upon some significant practical problems. They imply that variable intervals between successive applications of drugs and pesticides can be more effective in minimizing persistence time of parasites and pests.

Moreover, a rational strategy in pest control should integrate the use of chemical insecticides with biological control by natural enemies (Barclay, 1982). A major problem evolves as insecticides have often detrimental effects on the natural enemies of the pest (Legner & Medved, 1979). In many crop pests the young stage of both pest and its parasitoid is not exposed to the action of chemicals that are detrimental for adults. Application of the present model to these systems is therefore feasible. Following our theoretical conclusions it can be conjectured that a careful choice of the duration in which the pesticide is effective may selectively reduce the level of pest with regard to that of the natural enemy.

Implicit here is a phenomenon of self organization in biological systems, emerging from increasing variability in the environment (for comparison with thermodynamic systems, see Prigogine, 1978). However, this idea calls for further elaboration, using the notion of optimal life history strategies in varying environments (e.g. Agur, 1983).

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