

The Effect of Environmental Disturbances on the Dynamics of Marine Intertidal Populations

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A model is proposed for studying the influence of the duration of a nonreproducing life stage on the dynamics of marine intertidal populations. Analysis of the model shows that this system, in which the time delay (the nonreproducing stage) is in a density independent term, has two solutions. When the nonzero solution exists it is a stable point. A randomly occurring environmental disturbance, to which only the nonreproducing stage is resistant, is superimposed on the basic deterministic equation. Average extinction time, estimated by simulation, appears as a nonmonotonic function of the duration of disturbance. The graph of extinction time has multiple extrema with minima occurring where the ratio between the duration of the resistant stage and the duration of disturbance is an integer. This phenomenon is more sharply manifested when the intrinsic growth rate and frequency of disturbance are relatively large and when the variance in the duration of disturbance and the duration of the resistant stage is not too large. Increasing patchiness of the habitat has a minor effect on the pattern of dependence of the extinction time on the ratio between the juvenile and environmental periods. The suitability of the model for describing the marine intertidal system of the northern Red Sea is discussed, and it is suggested that the duration of the larval stage can determine adult population dynamics. © 1985 Academic Press, Inc.

1. INTRODUCTION

Many organisms have a nonreproducing life history stage which is resistant to external disturbances inflicted on the reproducing forms. Seeds of plants are relatively immune to extreme aridity. Eggs of various insects are less affected than other life stages by weather vagaries, parasites, etc. We

suggest that planktotrophic larvae of marine benthic invertebrates are another example of such an escape. Diffusing in the sea, these larvae are not susceptible to catastrophic wave action, which by tearing sessile adults from their beds or by covering inhabited patches with sand, can bring local adult populations on the shore to extinction.

The termination of the seed stage of annual plants and of the hibernating egg stage of some insects follows the end of their respective unfavorable seasons. In many other systems, the transition from a juvenile to an adult form is not determined by known periodic climatic signals. For pelagic larvae it was suggested that their longevity is determined by factors such as mixing in the onshore-offshore direction, length of the larval development period and mortality in the plankton (Jackson and Strathmann, 1981), maximization of recruitment per unit of reproductive effort (Vance, 1973; Palmer and Strathmann, 1981), individual selection for spreading siblings (Strathmann, 1974), habitat selection (Doyle, 1975), and maintenance of genetic continuity between distant populations (Scheltema, 1971). Mileikovsky, (1971) suggests that a longer mobile prereproductive stage increases dispersal and enables fast recuperation from critical reduction in population size.

Todd and Doyle (1981) propose the settlement-timing hypothesis according to which the duration of the pelagic stage may be determined so as to bridge the period between the optimal time to spawn and to settle. While stressing the significance for some species of the actual settling date, the same authors also note that other species have unpredictable timing of settlement, presumably due to stochastic environmental changes.

Stochastic environmental regimes greatly affect the dynamics of populations in general (Scheffer, 1951; Mech, 1966; Itô, 1980) and those of the marine intertidal populations in particular (Ayal and Safriel, 1982a,b; Paine, 1979). Under such conditions the existence in some species of an immune life stage is a bonus. However, this obvious benefit is traded off by a time delay in reproductive activity which causes an overall reduction in the intrinsic growth rate. Results of Parnas and Cohen (1976) imply that even for low frequency of disturbance the optimal duration of the resistant stage should be larger than the duration of an individual disturbance.

The relation between random environmental disturbances and the *duration* of the juvenile life stage is studied in the present article. Our approach is new in considering environmental stochasticity in the form of alternating *periods* of harsh and favourable conditions whose time scale may equal the biological time scale. By choosing this non-Markovian representation of the environment we deliberately sacrifice mathematical tractability for the sake of a more realistic description of many natural environments, whose variation can be approximated neither by deterministic models nor by stochastic white noise models.

The model attempts to give a specific description of the population dynamics of some marine intertidal molluscs in the northern Red Sea. We do not suggest that its precise form is a good description of all intertidal populations, or exclusively of intertidal populations. The main results reported here seem counterintuitive. In another work (Agur, in press) they are explored in a more general framework. The latter work shows that results presented hereafter are independent of the exact details of the deterministic equation, whereas the distribution of intervals between disturbances appears to determine the general pattern of extinction. For this reason the concepts presented here should be also appropriate for various other populations that live in regimes of random, relatively long, environmental disturbances to which only their nonreproducing life stage is invulnerable.

The article is organized in the following fashion. The deterministic model and its stochastic variant are outlined in the second section and the simulation results are presented in the third section. The motivation for making the various assumptions and the suitability of the model for describing marine intertidal dynamics are taken up in the discussion.

2. THE BASIC MODEL

2.1. *Population Growth in a Constant Homogeneous Environment*

The continuous growth of a single population with overlapping generations in a restricted environment is approximated by the well-known logistic equation

$$dx/dt = rx(1 - x/K). \quad (1)$$

The systems analyzed in the present work have the following 3 main characteristics:

- (1) A birth process with two stages: birth of juveniles—the planktonic larvae, and recruitment of juveniles to the adult population.
- (2) Recruitment is assumed to be the only density dependent element.
- (3) The juvenile stage provides a time-lag τ between birth and maturation.

Under these assumptions the increment to the adult population at time t will depend on 3 factors:

- (i) the birth of juveniles at time $t - \tau$, proportional to the number of adults at time $t - \tau$,
- (ii) the chances that juveniles born at time $t - \tau$, will survive to time t ,

(iii) the free resources available for adults which will determine the fraction of juveniles that will actually mature.

If $J(t - \tau)$ denotes a cohort of juveniles born at time $t - \tau$, during one time interval, then $J(t - \tau) = \lambda x(t - \tau)$, where λ is the birth rate and $x(t - \tau)$ is the number of adults at time $t - \tau$. The dynamics of this cohort is given by

$$dJ/dt = -\mu'J,$$

where μ' stands for the mortality rate of juveniles.

If τ is the duration of the juvenile stage then $J(t) = \lambda x(t - \tau) \exp(-\mu'\tau)$ will be the number of juveniles born at time $t - \tau$ that are ready to be recruited at time t . According to assumption (2) above the number of recruited individuals at time t will be

$$\lambda x(t - \tau) \exp(-\mu'\tau)(1 - x(t)/E),$$

where E is the environmental limiting factor. Adding now the deterministic term of adult mortality μ , and putting $x' = x/E$ and $\lambda' = \lambda \exp(-\mu'\tau)$ we obtain

$$dx'/dt = \lambda'x'(t - \tau)(1 - x'(t)) - \mu x'(t). \quad (2)$$

Note that whereas in the logistic model (Eq. (1)), equilibrium population size will be $x^* = K$, in Eq. (2) it will be $x^* = E(1 - \mu/\lambda')$. Having a different role, the environmental limiting factor was denoted E in Eq. (2) instead of the conventional K of the logistic equation. Figure 1 shows some characteristic time behaviour of Eq. (2) for different values of the parameters μ , λ' , τ . Equation (2) has one or two stationary states, $x' = 0$, $x' = 1 - \mu/\lambda'$,

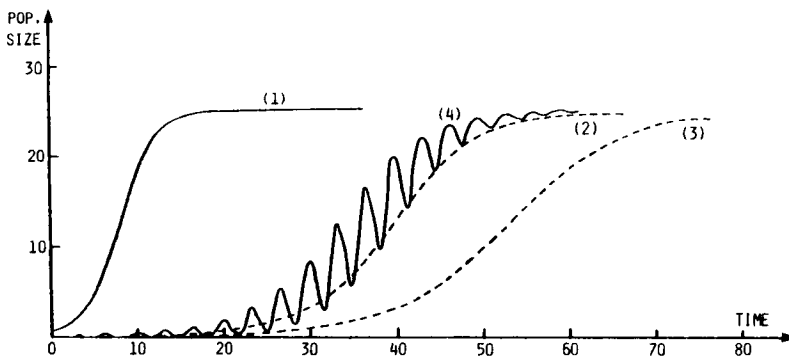


FIG. 1. Time evolution of x' , obtained by numerical simulation of Eq. (2). The parameter values are: $\lambda' = 1$, $\mu = 0.5$, $\tau = 0$ for (1); $\lambda' = 1$, $\mu = 0.5$, $\tau = 2$ for (2); $\lambda' = 1$, $\mu = 0.5$, $\tau = 3$ for (3); $\lambda' = 6$, $\mu = 3$, $\tau = 3$ for (4).

depending on the values of its parameters. Analysis of the linear stability of (2) around the stationary states is given in the Appendix, whereas numerical simulations of Eq. (2) are shown in Fig. 1.

2.2. Multipatch Environments

Equation (2) considers a single patch environment which is homogeneously affected by each disturbance. Hence, although its actual physical dimensions are not explicit in the present model, they must be considered small enough to justify the assumption of spatial homogeneity.

In Eq. (3) we extend the model to include multipatch environments that vary in the number of patches N and in their density.

$$dx'_i/dt = \sum_{j=1}^N \lambda' x'_j(t - \tau) g(s_{ji}, \tau)(1 - x'_i) - \mu x'_i, \quad i = 1 \text{ to } N. \quad (3)$$

In Eq. (3), $g(s_{ji}, \tau)$ is the probability of a juvenile with longevity τ that was hatched on patch j to arrive at patch i . Assuming Fick's law, $g(s_{ji}, \tau) ds = 1/\sqrt{4\pi d\tau} \exp(-(s_{ji} - c\tau)^2/2d\tau) ds$, where d is the diffusion coefficient, c is the drift coefficient, s_{ji} is the distance between patch j and patch i , and ds is the patch size. Equation (3) considers 1-dimensional diffusion between many small patches in a linear, relatively large, habitat (e.g., along the coasts of an ocean). We ignore diffusion in the perpendicular axis, assuming that its main effect is taken account of in the larvae mortality term. The values of the diffusion and drift coefficients in the mobility function $g(s_{ji}, \tau)$ were chosen such that the contribution of adults to subsequent recruitments in their own site is considerably large. This assumption is justified in areas such as the Gulf of Eilat in the Red Sea, where available patches are very distant from each other and are often located in the inner part of lagoons with narrow openings into the sea (Ayal and Safriel, 1982b). Obviously the exact form of $g(s_{ji}, \tau)$ can be adjusted to other modes of dispersal, but this function is expected to be of secondary importance in the model. It should be noted that Eq. (2) is a special case of Eq. (3) for $N = 1$, and $g(s_{ji}, \tau) = 1$.

2.3. Stochastic Environment

Disturbances are assumed to cause an instantaneous death of a fraction Δ of the adult population, where $0 < \Delta \leq 1$. Their duration is constant or normally distributed, with an average value δ . The times between the end of one disturbance and the beginning of the next one are independent exponentially distributed random variables with a mean $1/\varphi$ (stochasticity of this kind is conventionally called "telegraphic noise"). It should be noted that the assumption of random occurrence of disturbances is a basic property of the model. This is demonstrated elsewhere (Agur, in press), where simulation experiments in an environment with a periodic distribution of intervals show

different results than those in an environment with exponentially distributed intervals.

In the computer simulation the stochastic process was coupled with the deterministic population growth using the following procedure. In each simulation experiment Eq. (2) or Eq. (3) was integrated by the Euler method. At the same time a stochastic generator was activated *for each patch independently* in order to determine the times of the initiation of the disturbances. The time unit of integration was of the order of magnitude of $\tau/100$, and the population was defined as extinct when its numbers remained negligibly small (less than 1×10^{-7} of the initial population size) for a period equal to τ . Each simulation experiment was iterated 100 times and the average time to extinction was estimated for that population-environment set (for the use of the average time to extinction as a measure of success, see e.g., Ludwig, 1978; Hanson and Tuckwell, 1981).

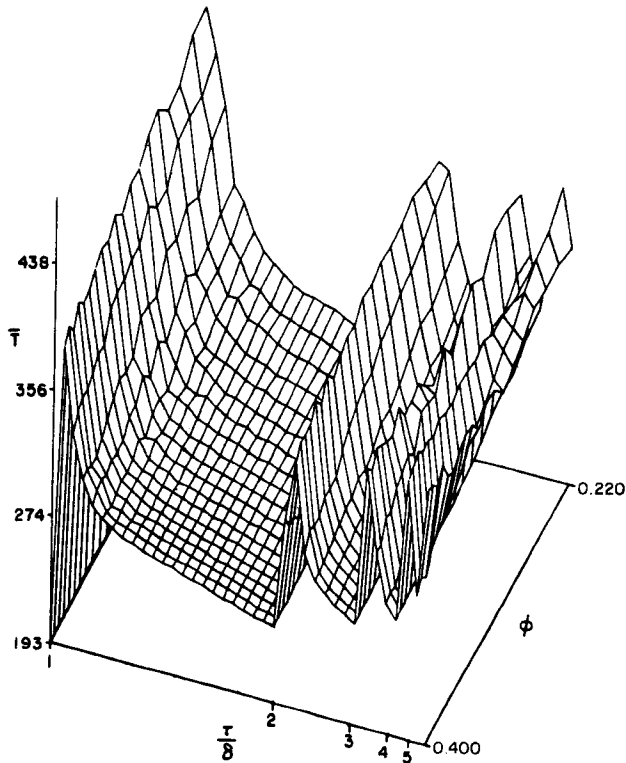


FIG. 2. Average extinction time of the population, \bar{T} , is plotted as a function of τ/δ for different values of disturbance frequency. $A = 1$, $\lambda = 0.05$, $\mu' = 0.01$, $\mu = 0.01$, $\tau = 90$, $\delta = 18-90$, $I = 50$, $E = 100$, $N = 1$, $\phi = 0.22-0.4$. Each point in the graph is an average of 100 simulations of Eq. (2) with the telegraphic noise superimposed.

3. RESULTS

Figures 2–6 show simulation results of population dynamics in a single homogeneous patch whose initial population size is I and its environmental limiting factor is E (Eq. 2) (I and E were kept constant in all simulations; δ and τ were kept constant in all simulations except when stated otherwise).

Figure 2 and Figure 3 show how the time to extinction of the population is affected by the duration of disturbance δ , its frequency ϕ and its magnitude Δ . We expected the extinction time to be some decreasing function of δ , since a larger δ , for fixed ϕ and τ , corresponds to a higher proportion of time under inhospitable conditions. Contrary to our expectations, however, when $\Delta = 1$, simulation results consistently show a minimum in the average extinction time for $\tau/\delta = 2$. Additional minima occur for $\tau/\delta = 3, 4, 5, \dots$, when the frequency of disturbance ϕ is not too small. Decreasing magnitude of the disturbance increases the average extinction time for all values of τ/δ .

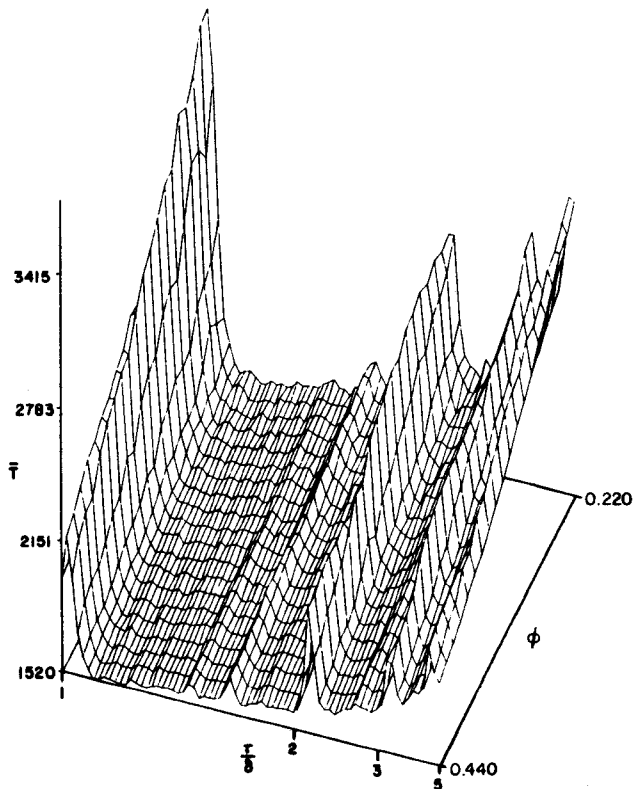


FIG. 3. As in Fig. 2, but $\Delta = 0.3$.

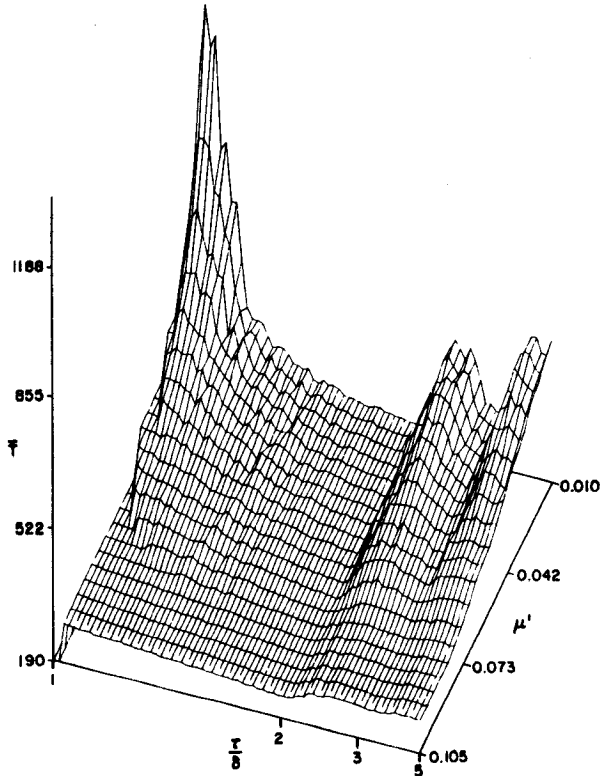


FIG. 4. The influence of the juvenile mortality rate on the extinction time of the population. Average extinction time \bar{T} is plotted as a function of τ/δ for different values of μ' . $\lambda = 1$, $\varphi = 0.05$. Other parameters as in Fig. 2.

Still, the general nonmonotonic pattern is preserved when Δ varies between 1.0 and 0.3, with additional less significant maxima emerging with decreasing Δ (Fig. 3). Having the same "macro" effect, with a slightly less complex general behaviour, we kept $\Delta = 1$ in all simulation experiments whose description follows hereafter.

In Figure 4 we varied juvenile mortality μ' while keeping the frequency of disturbance constant. The nonmonotonic dependence of the average extinction time on the relation τ/δ appears to be independent of the juvenile mortality rate. However the maxima are much less pronounced when juvenile mortality is large. Variation in λ (not shown here) has a similar effect: the general pattern of the extinction time curve is preserved but the nonmonotonic behaviour is less significant when λ is small. Variation in adult mortality μ has practically no effect on the general pattern.

Figure 5 shows simulation results with a Gaussian variance about δ . In

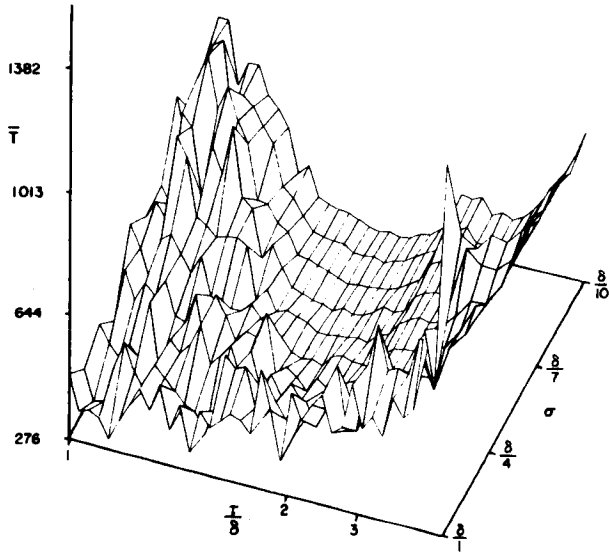


FIG. 5. Gaussian variance about δ is introduced in the simulations. The pattern of change in extinction time as a function of δ is influenced by variance about δ when σ is relatively large. $\lambda = 1$, $\varphi = 0.1$. Other parameters as in Fig. 2.

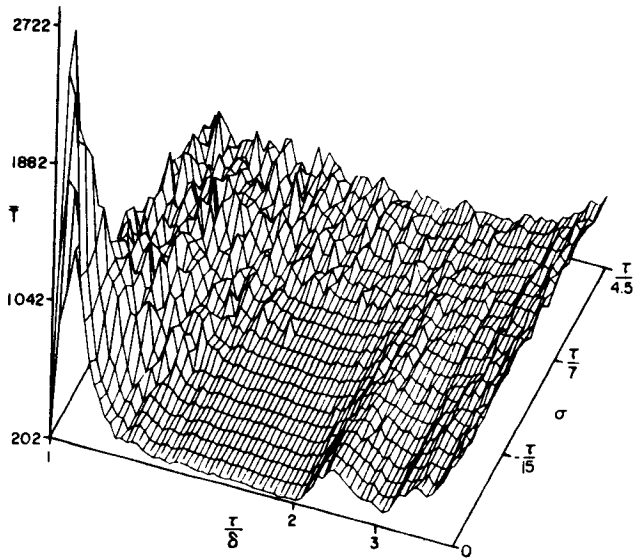


FIG. 6. As in Fig. 5 for variance about τ .

Fig. 6, δ is again constant while a Gaussian variance is introduced now about τ . Simulations show that when variance about δ or τ is not too large ($\sigma \leq \delta/7$ or $\sigma \leq \tau/7$), the system still has a clear minimum in the average time to extinction for $\tau/\delta = 2$, and a clear maximum for $\tau/\delta \rightarrow 1$. The minima in the average extinction time for $\tau/\delta = 3, 4, 5, \dots$, are slightly less prominent when σ is relatively large and when $\sigma \geq \delta/4$ or $\sigma \geq \tau/5$, average extinction time is low over the whole range of τ/δ , with no distinguishable extrema.

In order to study the effect of spatial heterogeneity of the habitat on the persistence of the population, the original habitat is divided into N patches with various distances between them. The initial population size and the environmental limiting factor for each individual patch are now I/N and E/N , and as was mentioned above, disturbance occur independently in each patch. Simulation results, (Fig. 7) show a large increase in extinction time with increasing number of patches for all values of τ/δ . However the general pattern of a nonmonotonic dependence of the extinction time on τ/δ is preserved when increasing the number of patches. Simulation results for

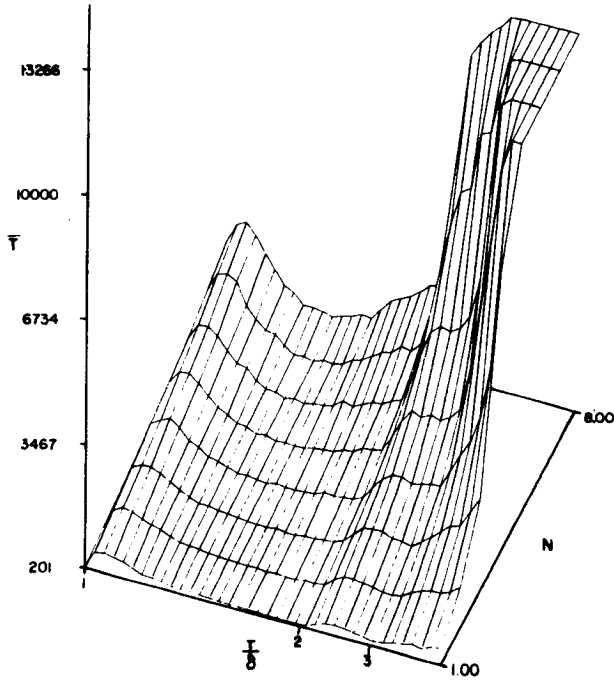


FIG. 7. Simulation results of Eq. (3) with the telegraphic noise showing the effect of habitat patchiness on the extinction time of the population. Total carrying capacity, $E = 100$, and the total initial population size, $I = 50$, are equally divided between patches. $\lambda = 2$, $\varphi = 0.05$, habitats length $= N \times 5$. Fick's law is assumed for $g(s, \tau)$, with $d = 0.1$, $ds = 1$, $c = 0$.

various values of the drift coefficient (not presented here) show that strong drift reduces the average extinction time in general but has no qualitative effect on the pattern of its dependence on the relation τ/δ .

4. DISCUSSION

Analysis of the basic deterministic model (Eq. 2) shows that the conditions for existence and stability of the two stationary states are not qualitatively different from those of the simple logistic equation. The only difference between the original logistic equation and its present time delay version, is that in the latter, damped oscillations are superimposed on the normal logistic growth (Fig. 1). In contrast to models in which the time delay appears in the density dependent term (Hutchinson, 1948; May 1974), the system presented here is intrinsically stable.

Environmental uncertainty in the form of a multiplicative telegraphic noise was superimposed on the basic deterministic equations. From the simulation results it appears that the time to extinction is not a monotonically decreasing function of the duration of disturbance. Rather, there appears to be a resonance effect, by which when the frequency of disturbance is large, the chances of persistence are minimized for $\tau/\delta = n$ ($n = 1, 2, 3, \dots$) and maximized for $\tau/\delta \rightarrow n$.

This phenomenon, studied in detail elsewhere (Agur, in press) can be briefly explained as follows: when $1 < \tau/\delta \leq 2$, and $\Delta = 1$, juveniles born in a given interval can be recruited to the adult population in the following interval only. Consequently for the population to become extinct it suffices that one episode of recruitment is fully overlapped by a disturbance. As the probability of initiation of a new disturbance is constant over time, the chances that such an overlap will occur increase with increasing "wasted time" between the end of one disturbance and the beginning of the following recruitment episode. In the region $1 < \tau/\delta \leq 2$, the fraction of "wasted time" is maximized for $\tau/\delta = 2$. It follows that extinction probability in this region is maximized, and the average extinction time is minimized, for $\tau/\delta = 2$. In the same spirit one can show that when the frequency of disturbance is large, extinction chances in the region $2 < \tau/\delta \leq 3$ are maximized for $\tau/\delta = 3$, etc.

Extinction for $\Delta < 1$ is realized through multiple repetitions of the sequence which causes extinction for $\Delta = 1$. Hence, although extinction time increases with decreasing Δ , the value of Δ has no effect on the probability of occurrence of this sequence. It should be mentioned that we have no analytic explanation for the additional maxima which appear in the region $1 < \tau/\delta \leq 2$ for $\Delta < 1$.

It is suggested here that the time to extinction of a single isolated patch,

subjected to environmental variation is mostly influenced by the ratio τ/δ . In an archipelago local extinction is only one of two distinguishable processes that determine the time to extinction of the whole population. The other process is recolonization by juveniles arriving from adjacent sites. Recolonization ability should depend on the flow in the system, and on the coincidence of a favourable period in an empty site, with the availability of juveniles produced in another site τ time units earlier. The chances of this coincidence should be positively related to τ/δ . For this reason increased patchiness has little effect on the extinction time when τ/δ is relatively small.

Our results indicate that for disturbance magnitude not smaller than 0.3, when the variance about δ and τ is not too large, and when the intrinsic growth rate and the frequency of disturbance are large, it is the degree of adaptation of the biological parameter—the duration of the resistant stage—to the environmental parameter—the duration of disturbance—which principally determines the extinction time. That variance in the duration of the larval stage can be very large is indicated by Jackson and Strathmann (1981), but a good fit between the brooding and the settlement seasons, found for two intertidal barnacles (Hines, 1981), does not exclude the possibility that at least some species have little variance in τ . The rate of recruitment, determined principally by λ and μ' , plays an important role here; it has to be relatively large for the wavelike pattern in the average extinction time curve to be strongly manifested. The direct measurements of larval mortality rates are notoriously difficult, but daily estimates cited by Jackson and Strathmann (1981) range from 0.018 for *Panulirus interruptus* to 0.33 for *Balanus balanoides*. According to a general estimate of these writers, mortality rates of invertebrates with a precompetent period of several weeks or more correspond to those appearing in the central part of the juvenile mortality range presented in Fig. 4. In the Gulf of Suez in the Red Sea larvae of sibling species largely vary in their life span, in spite of their similar sizes and overlapping period in the plankton (Ayal and Safriel, 1982a). One may infer then that in many natural systems juvenile mortality is not expected to damp too severely the nonmonotonic phenomenon observed theoretically, and that mortality in the plankton, whether stochastic or deterministic is not a dominant factor in determining the duration of the larval stage. Having shown theoretically that persistence depends on the relation between the juvenile stage longevity and the duration of disturbance inflicted on adults, we suggest that persistence of intertidal populations is affected by the relation between the larval period and the period of disturbance for the benthic forms. It may be inferred, then, that stochasticities in the environment of the benthic forms may have an important role in determining the duration of the larval period.

Environmental uncertainty is well reflected in the high temporal fluctuations in the adult population size of intertidal species in the Red Sea

(Ayal and Safriel, 1982a,b). Exposure to waves, sand suffocation or isolation, and drainage of tidal pools from the sea may cause a massive local population destruction. The stochastic mortality factors can be of variable magnitude at different times and in adjacent patches. In the Gulf of Eilat in the Red Sea, storms that last on the average 2 days tear benthic molluscs from their base, and cover individual patches of populated intertidal rock with sand that usually remains up to 4 months. This sand brings about suffocation of most of the adults and prevents settlement of larvae (A. Genin, personal communication).

Populations of planktonic larvae tend to fluctuate following changes in temperature or in food supply (Itô, 1980). In the Red Sea settlement is affected by hazardous water currents (Ayal and Safriel, 1982a,b). However, the sources of fluctuations in the larval and adult media are not usually assumed to be related. In places where recruitment is strictly limited by shortage of settling area, stochasticity in the pelagic stage is expected to have a negligible effect on population dynamics. We believe that the effects on the optimal duration of the larval stage of stochasticity in the planktonic and in the benthic periods are nonexclusive, although, in some cases they may be contradictory. We support this idea by an example from the Red Sea, where longer planktotrophic period is associated with a higher abundance and a higher stability of the benthic population.

The two sympatric sibling cerithiid gastropods, *Cerithium scabridum* and *Cerithium caeruleum* show a marked difference in the duration of the periods which their larvae spend in the plankton (45–60 days for *C. scabridum* vs 90–120 days for *C. caeruleum*). Ayal and Safriel (1981, 1982a,b) studied the dynamics of these species in the Gulf of Suez and the Gulf of Eilat in the Red Sea. In the Gulf of Suez, *C. caeruleum* has a relatively stable population while *C. scabridum* shows high fluctuations in its sessile population size. The latter species is almost totally excluded from the Gulf of Eilat habitat which, although similarly unpredictable locally, is characterized by a higher isolation of individual patches. *C. caeruleum* has a patchy, single age group, distribution in the Gulf of Eilat. It seems plausible then that the higher variation in yearly recruitment of *C. scabridum* in the Gulf of Suez and its almost total exclusion from the Gulf of Eilat is due to its larval stage being too short to bridge over 4 months long disturbances that are typical to this gulf.

Palmer and Strathmann (1981) suggest that increased scale of dispersal renders little benefit to long-lived larvae and thus cannot explain the advantage of planktotrophy (longer period in the plankton) over lecithotrophy. Strathmann (1980) suggests that larvae serve for damping spatial and temporal variations in favourability of adults sites. The same view is expressed in the present work: we conjecture that the longevity of the larval life, in regimes of harsh and frequent disturbances, is mainly deter-

mined by the duration of disturbance in the location of recruitment. Hence increased dispersal of larvae, bearing no advantage of its own, may sometimes be a side effect of adaption that enables larvae to buffer local extinction of the benthic animals, caused by disturbances that prevent recruitment during a relatively long period.

5. CONCLUSIONS

Our model is characterized by the description of the population dynamics in a harshly varying environment as being an outcome of two processes: the population process determined by the resistant stage, and the environmental process determined by the durations of alternating harsh and favourable episodes. The special synchronization phenomenon that appears in the results is expected to be manifested when variance in τ/δ is relatively small and when the intrinsic growth rate and the frequency of disturbance are relatively large. The counterintuitive character of our theoretical results may render them able to explain some as yet mysterious life history strategies. Thus it seems worthwhile to examine such strategies on the background of a quantified environmental pattern.

6. APPENDIX: STABILITY ANALYSIS OF EQUATION (2)

In the stability analysis of Eq. (2) we show that the first stationary state $x' = 0$ is unstable and that the other one $x' = 1 - \mu/\lambda'$, is locally stable. The latter has a biological significance only if $\lambda' > \mu$. The linearized equation around $x' = 0$ is

$$d\delta x'/dt = \lambda' \delta x'(t - \tau) - \mu \delta x'. \quad (\text{A1})$$

The characteristic equation for the eigenvalues $\omega = \omega_r + i\omega_i$ of (A1) is

$$\begin{aligned} \omega_r &= \lambda' \exp(-\omega_r \tau) \cos(\omega_i \tau) = \mu \\ \omega_i &= -\lambda' \exp(-\omega_r \tau) \sin \omega_i \tau. \end{aligned} \quad (\text{A2})$$

It is easy to see that for the choice $\omega_i = 0$ there exists a solution of (A2) with $\omega_r > 0$, hence instability of $x' = 0$. Note that this particular solution of (A2), has no oscillations near the stationary state and represents the fastest growth rate (see also Fig. 1).

The linearized equation around $x' = 1 - \mu/\lambda'$ is

$$d\delta x'/dt = \mu \delta x'(t - \tau) - \lambda' \delta x'. \quad (\text{A3})$$

The characteristic equation is then

$$\begin{aligned}\omega_r &= \mu \exp(-\omega_r \tau) \cos(\omega_i \tau) - \lambda' \\ \omega_i &= -\mu \exp(-\omega_r \tau) \sin(\omega_i \tau).\end{aligned}\tag{A4}$$

Employing the condition $\lambda' > \mu$ one sees immediately from the first equation in (A4) that every solution of (A4) satisfies $\omega_r < 0$, hence local stability of $x' = 1 - \mu/\lambda'$.

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REFERENCES

- AGUR, Z. Randomness, synchrony and population persistence, *J. Theor. Biol.*, in press.
- AYAL, Y., AND SAFRIEL, U. N. 1981. Species composition, geographical distribution and habitat characteristic of rocky intertidal Cerithidae (Gastropoda, Prosobranchia) along the Red-Sea shores of Sinai, *Isr. J. Malacol.* **7**, 53-72.
- AYAL, Y., AND SAFRIEL, U. N. 1982a. *r*-curves and the cost of the planktonic stage, *Amer. Nat.* **119**, 391-401.
- AYAL, Y., AND SAFRIEL, U. N. 1982b. Role of competition in determining habitat occupancy of Cerithidae (Gastropoda: Prosobranchia) on the rocky, intertidal, Red-Sea coasts of Sinai, *Mar. Biol. (Berlin)* **68**, 1-12.
- DOYLE, R. W. 1975. Settlement of planktonic larvae: a theory of habitat selection in varying environments, *Amer. Nat.* **100**, 113-127.
- HANSON, F. B., AND TUCKWELL, H. C. 1981. Logistic growth with random density independent disasters *Theor. Popul. Biol.* **19**, 1-10.
- HINES, A. H. 1979. The comparative reproductive ecology of three species of intertidal barnacles, in "Reproductive Ecology of Marine Invertebrates" (S. E. Stancyle, Ed.), *Belle W. Baruch Lib. Mar. Sci.* **9** 213-234.
- HUTCHINSON, G. E. 1948. Circular causal systems in ecology, *Ann. N.Y. Acad. Sci.* **50**, 221.
- IRÔ, Y. 1980. "Comparative Ecology," Cambridge Univ. Press, London/New York (English transl.).
- JACKSON, G. A., AND STRATHMANN, R. R. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development, *Amer. Nat.* **118**, 16-26.
- LUDWIG D. 1978. Comparison of some deterministic and stochastic population theories. in "Population and Communities" (S. A. Levin, Ed.), pp. 367-388, MAA Studies in Mathematics, Math. Assn., Washington, D. C.
- MAY, R. 1974. "Stability and Complexity in Model Ecosystems," Monographs in Population Biology, Princeton Univ. Press, Princeton, N.J. (2nd ed.).
- MECH, L. D. 1966. "The Wolves of Isle Royal," Fauna of the National Parks U. S. No. 7, U. S. Govt. Printing Office, Washington, D. C.
- MILEIKOVSKY, S. A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: A reevaluation, *Mar. Biol. (Berlin)* **10**, 193-213.

- PAINÉ, R. T. 1979. Disaster, catastrophe, and local persistence of the sea palm, *Postelsia palmaeformis*, *Science (Washington, D. C.)* **205**, 685-687.
- PALMER, A. R., AND STRATHMANN, R. R. 1981. Scale of dispersal in varying environments and its implications for life histories of marine invertebrates, *Oecologia* **48**, 308-318.
- PARNAS, H., AND COHEN, D. 1976. The optimal strategy for the metabolism of reserve materials in micro-organisms, *J. Theor. Biol.* **56**, 19-55.
- SCHEFFER, B. B. 1951. The rise and fall of a reindeer herd, *Sci. Mon.* **73**, 356-362.
- SCHELTEMA, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow water benthic marine gastropodes, *Biol. Bull. Marin. Lab. Biol. Woods Hole*, **140**, 284-322.
- STRATHMANN, R. 1974. The spread of sibling larvae of sedentary marine invertebrates, *Amer. Nat.* **108**, 29-45.
- STRATHMANN, R. R. 1980. Why does a larva swim so long? *Paleobiology*, **6**, No. 4, 373-376.
- TAYLOR, F. 1980. Timing in the life histories of insects, *Theor. Popul. Biol.* **18**, 125-133.
- TODD, C. D., AND DOYLE, R. W. 1981. Reproductive strategies of marine benthic invertebrates: A settlement timing hypothesis, *Mar. Zool. Prog. Ser.* **n**, 75-83.
- VANCE, R. R. 1973. On reproductive strategies in marine benthic invertebrates, *Amer. Nat.* **107**, 339-352.