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PATTERNS OF DYNAMICAL BEHAVIOUR IN SINGLE-SPECIES POPULATIONS

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INTRODUCTION

The original view that density dependent mortality or natality must contribute to stability in single-species populations (Howard & Fiske 1911; Smith 1935; Nicholson 1933 and others), has more recently given way to a more detailed understanding of density dependence and its effects on population stability. It is now appreciated that density dependence alone cannot only lead to stable equilibria, but also can lead to patterns of stable cyclic oscillations (with period and amplitude determined by the intrinsic biological parameters), and even to irregular and apparently 'chaotic' population fluctuations. Such patterns can arise in populations with continuously overlapping generations (modelled by differential equations) provided that there are sufficiently long time delays in the density dependent mechanism. They arise more readily in populations with discrete, non-overlapping generations (difference equations), where this rich spectrum of dynamical behaviour can arise in the very simplest of non-linear models (see, for example, May 1974; May *et al.* 1974; Li & Yorke 1975; May & Oster 1976).

In this paper we survey a variety of data from field and laboratory populations with (approximately) discrete generations, and fit all such data to a simple density dependent population model. The model parameters arising from this fit are then examined, in order to compare the kinds of stability behaviour that are most frequently found in real populations with the kinds of behaviour known to be theoretically possible in such population models.

In assembling such data for single-species populations, two qualitatively different situations should be distinguished. Laboratory studies have the advantage that there really is a good approximation to a single-species situation (homogeneous environment, constant food supply, no competitors nor predators). But because laboratory populations are liberated from many of the shocks and hazards they may suffer in the outside world, they may exhibit an exaggerated tendency towards 'boom' and consequent 'bust'. Conversely, field studies on natural populations have the disadvantage that a single-species description is at best an approximation, in which dynamical interactions with food supply, competitors, parasites and predators are replaced by passive single-species population parameters. In the worst cases, for example where the basic dynamical feature is a predator-prey cycle, such a process of 'averaging out' the predator to arrive at a single-species description will give a most misleading impression of the dynamics; this point is developed more fully below.

We now proceed to define and discuss the single-species population model we use, and to describe the sorts of available data. The main section then discusses the results obtained from life-table data on natural populations, from laboratory experiments, from

information on the magnitude of observed population fluctuations, and merely from estimates of the rate of population increase, λ . The main results are summarized in Figs 2 and 5; the concluding section discusses these results, and emphasizes various directions in which the present study is oversimplified.

MODELS

Our analysis can be carried out most precisely by reference to an appropriate single-species population model. We shall use the model discussed by Hassell (1975), namely

$$N_{t+1} = \lambda N_t (1 + a N_t)^{-\beta}, \quad (1)$$

where N_t and N_{t+1} are the populations in successive generations, λ is the finite net rate of increase and a and β are constants defining the density dependent feedback term. This model is but one example from a family of similar difference equation models with two or three parameters (see Table 1 of May & Oster (1976)).

The examples in Fig. 1 show the form of the density dependent function from eqn (1)

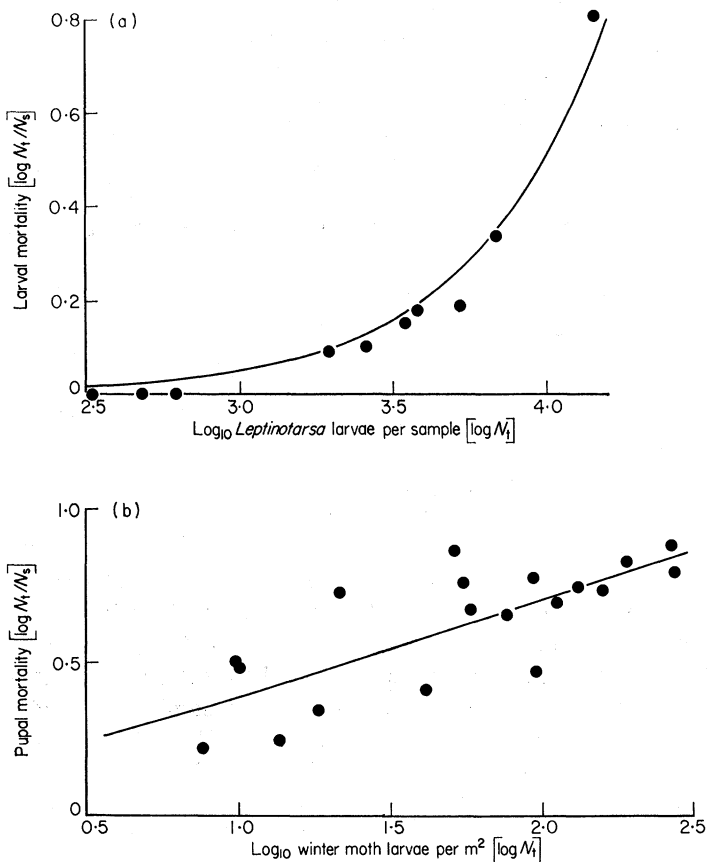


FIG. 1. Density dependent relationships described by eqn (1). (a) Larval starvation in the Colorado potato beetle (*Leptinotarsa decemlineata*); $a < 0.00007$, $\beta > 30$ (data from Harcourt 1971). (b) Pupal mortality of the winter moth (*Operophtera brumata*); $a = 0.6$, $\beta = 0.4$ (data from Varley & Gradwell 1968).

fitted to data for the levels of starvation at different densities of Colorado potato beetle larvae (*Leptinotarsa decemlineata* (Say)) (Harcourt 1971) and to pupal mortality of the winter moth (*Operophtera brumata* L.) (Varley & Gradwell 1968). The mortality is expressed as $\log N_t/N_s$ (where N_s is the number of surviving larvae in generation t) plotted against population size ($\log N_t$). In this form, the data are well described using the equation

$$\log N_t/N_s = \beta \log (1 + aN_t), \quad (2)$$

which is related simply to eqn (1) because $N_{t+1} = \lambda N_s$. From eqn (2) we see that β is the slope of the relationship attained at high population densities and that a is related to the

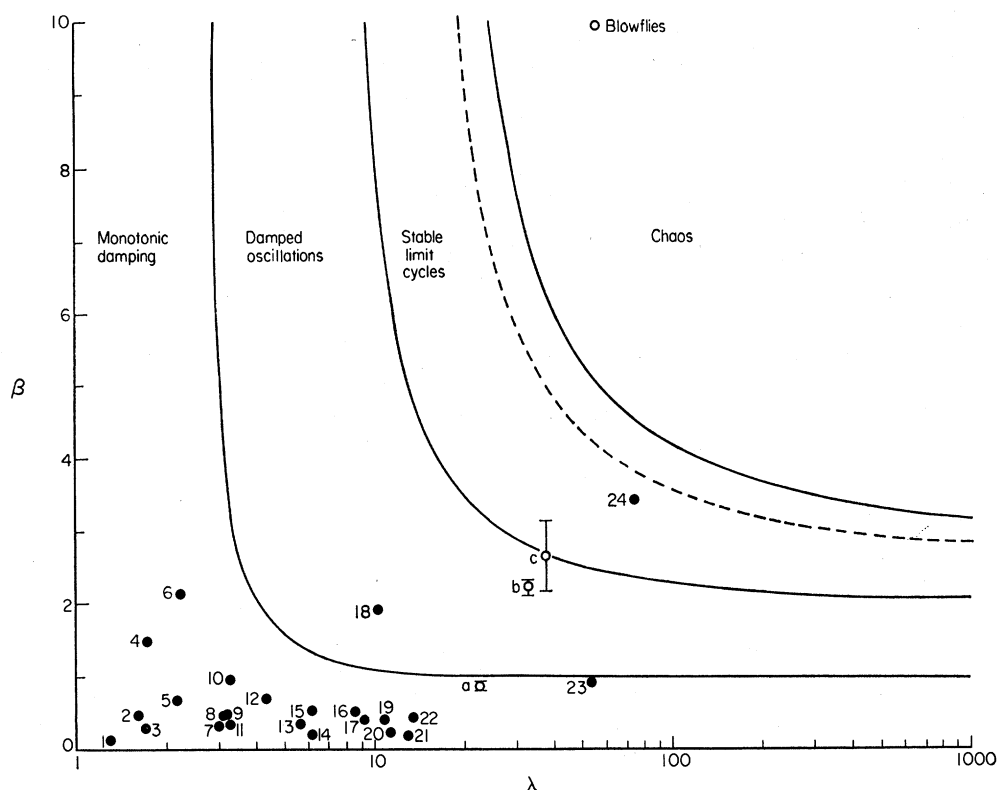


FIG. 2. Stability boundaries between the density dependent parameter, β , and the population growth rate, λ , from eqn (1). The solid lines separate the regions of monotonic and oscillatory damping, stable limit cycles and chaos. The broken line indicates where two-point limit cycles give way to higher order cycles. The solid circles come from the analyses of the life table data in Table 1 and the number by each point refers to this table. The hollow circles are discussed under 'Laboratory experiments'.

point of inflection of the curve. Thus varying values of β describe competition for resources, which ranges from 'scramble' ($\beta \rightarrow \infty$) to 'contest' ($\beta \rightarrow 1$).

The dynamical behaviour of this model may be elucidated by the techniques outlined in May & Oster (1976). These graphical methods show that for eqn (1) the global and local stability of the equilibrium point (i.e. the point where $N_{t+1} = N_t = N^*$) march together. The local stability of N^* depends on the slope of the function on the right-hand side of eqn (1) at N^* , and this linearized stability analysis for eqn (1) is discussed

fully in Hassell (1975). We thus can find the domain of parameter space wherein the global behaviour is a stable point, with monotonic damping or with oscillatory damping (see Fig. 2). The boundaries where stable two-point cycles give way to stable four-point cycles, and eventually where the entire bifurcating hierarchy of stable cycles of period 2^n give way to chaotic dynamics, requires an ineluctably non-linear analysis. The methods are indicated in May & Oster (1976), where, in particular, a rapidly convergent iterative algorithm for finding the boundary between cycles and chaos is given. These techniques provide the other stability boundaries illustrated in Fig. 2.

THE DATA

With Fig. 2 in mind, our aim is to pin-point the stability regions in which natural populations are most likely to fall. We shall draw upon four main classes of data.

(1) Life-table data from insect populations with discrete generations, as shown in Table 1. This is the most complete information available to us, but at the same time is only representative of a particular kind of life history, and of populations that are relatively easy to sample. Life-table data from other taxa, particularly birds (e.g. Blank, Southwood & Cross 1967; Krebs 1970; Southern 1970) and mammals (e.g. Sinclair 1973), have been excluded since generations overlap, making so simple a model as eqn (1) inappropriate.

(2) Population changes in cultures of single insect species maintained in the laboratory.

(3) The magnitude of observed population fluctuations (from maxima to minima). These are compared with the ranges known to occur in the regions of stable limit cycle or chaotic behaviour predicted from eqn (1).

(4) Estimates of the rate of increase, λ . These, by themselves, set limits on the range of possible stability behaviour.

RESULTS

Life-table data

The solid circles in Fig. 2 are all derived from the analysis of life table data of the populations listed in Table 1. These are all instances where density dependence has been identified at some stage in the life cycle, enabling an estimate of β to be obtained. As indicated above, this is done by plotting mortality (as $\log N_t/N_s$) against population density as ($\log N_t$), and using a least squares technique to fit eqn (2) to the data. In most cases, the least squares technique provides a good description of the data, as shown by the two examples in Fig. 1. In order to get a simple estimate of the confidence limits on β , the data were transformed into linear form by fixing a as initially found, and then calculating the linear expression of $Y = \log N_t/N_s$ against $X = \log (1 + aN_t)$. This value of β (which was always very similar to the initial least squares estimate), is shown in Fig. 2 and listed, together with its confidence limits, in Table 1.

The estimates of λ for Fig. 2 depend, in the first place, upon knowing the average maximum fecundity per adult. This value is then reduced in proportion to the sum of the averages of all the density independent mortalities acting during the life cycle. In this way, λ becomes the net rate of increase of the population from generation to generation, for which the density dependent mortality must compensate. Table 2 illustrates this procedure for the winter moth data of Varley & Gradwell (1968), showing the assumed

Table 1. Estimates of β and λ , and their 95% confidence limits, from the analysis of insect life table data; numbers correspond to the numbered points in Fig. 2

No.	Species	β	λ	Author
1	Moth: <i>Zeiraphera diniana</i> Gn.	0.1 (0.0-0.2)	1.3 (0.4-4.2)	Auer (1968)
2	Bug: <i>Anthocoris confusus</i> (Reuter)	0.5 (0.1-1.3)	1.6 (2.1-8.8)	Evans (1973)
3	Beetle: <i>Phytodecta olivacea</i> (Forst.)	0.3 (0.1-0.4)	1.7 (0.9-3.2)	Richards & Waloff (1961)
4	Moth: <i>Hyphantria cunea</i> Drury	1.5 (1.4-1.6)	1.7 (0.8-3.8)	Itô, Shibasaki & Iwahashi (1969)
5	Scale: <i>Parlatoria oleae</i> (Colvee)	0.7 (-0.3-1.6)	2.2 (1.4-3.3)	Huffaker & Kennett (1966)
6	Bug: <i>Leptoterna dolabrata</i> (L.)	2.1 (0.9-3.3)	2.2 (0.9-3.2)	McNeill (1973)
7	Moth: <i>Erannis defoliaria</i> (Clerk)	0.4 (0.0-0.7)	3.0 (1.8-5.1)	Ekanayake (1967)
8	Moth: <i>Bupalus piniarius</i> L.	0.5 (0.1-0.8)	3.1 (2.1-4.6)	Klomp (1966)
9	Parasitoid fly: <i>Cyzenis albicans</i> (F.)	0.5 (0.3-0.7)	3.2 (1.3-8.0)	Hassell (1969)
10	Fly: <i>Erioischia brassicae</i> (L.)	1.0 (0.7-1.3)	3.3 (1.2-9.0)	Mukerji (1971)
11	Moth: <i>Cadra cautella</i> Walk.	0.3 (0.1-0.6)	3.3 (1.4-7.7)	Benson (1974)
12	Bug: <i>Nezara viridula</i> L.	0.7 (0.1-1.3)	4.3 (2.1-8.8)	Kiritani, Hokyo & Kimura (1967)
13	Moth: <i>Operophtera brumata</i> (L.)	0.3 (0.2-0.5)	5.5 (3.2-9.3)	Varley & Gradwell (1968)
14	Bug: <i>Nephotettix cincticeps</i> Uhler	0.2 (0.1-0.3)	6.1 (3.6-10.4)	Kiritani <i>et al.</i> (1970)
15	Moth: <i>Erannis progemma</i> (Hb.)	0.5 (0.1-1.0)	6.3 (4.0-10.0)	Ekanayake (1967)
16	Moth: <i>Anagasta kuehniella</i> (Zell.)	0.5 (0.3-0.7)	8.6 (7.3-10.1)	Hassell & Huffaker (1969)
17	Bug: <i>Neophilaenus lineatus</i> (L.)	0.4 (0.3-0.5)	9.2 (7.5-11.4)	Whittaker (1971)
18	Mosquito: <i>Aedes aegypti</i> (L.)	1.9 (0.7-3.1)	10.6 (6.4-17.5)	Southwood <i>et al.</i> (1972)
19	Moth: <i>Tyria jacobaeae</i> L.	0.4 (0.1-0.7)	10.7 (1.6-72.4)	Dempster (1975)
20	Moth: <i>Erannis leucophaearia</i> (Schiff.)	0.2 (0.0-0.5)	11.2 (7.6-16.6)	Ekanayake (1967)
21	Moth: <i>Acleris variana</i> Fern.	0.2 (0.0-0.4)	13.0 (6.2-27.1)	Morris (1959)
22	Bug: <i>Saccarosydne saccharivora</i> (Ww.)	0.4 (0.1-0.7)	13.5 (7.8-23.5)	Metcalfe (1972)
23	Parasitoid wasp: <i>Bracon hebetor</i> Say	0.9 (0.4-1.4)	54.0 (27.1-107.8)	Benson (1974)
24	Beetle: <i>Leptinotarsa decemlineata</i> (Say)	3.4 (2.5-4.3)	75.0 (44.2-127.3)	Harcourt (1971)

maximum fecundity of 100 eggs per adult moth reduced to a value of $\lambda = 5.5$. The confidence limits for λ given in Table 1 are simply obtained from the variance of the mean total density independent mortality per generation. The variance in the fecundity per adult was not included since most life table studies have not given this information.

Figure 2 shows almost all the points from the life-table analyses to have stable equilibria and to lie in the region of monotonic damping. There is only one point, that of the Colorado potato beetle (*Leptinotarsa*), that has an unstable equilibrium and clearly falls

Table 2. Calculation of the net rate of population increase (λ) for the winter moth (*Operophtera brumata*); data from Varley & Gradwell (1968)

Average natality	
Average egg compliment per female	= 200
Sex ratio	= 1:1
Average fecundity per adult	= 100
Average density independent mortality	
(expressed as $\log_{10} N_t/N_0$)	
Between adult and prepupal stages	= 1.02
(excluding larval parasitism)	
Due to the parasitoid, <i>Cyzenis albicans</i>	= 0.03
Due to a microsporidian disease	= 0.03
Due to other larval parasitoids	= 0.03
Due to the pupal parasitoid, <i>Cratichneumon culex</i> (Muel.)	= 0.15
Total	1.26 ± 0.23 (95% limits)

Thus $\log_{10} \lambda = \log_{10} 100 - 1.26 = 0.74 (\pm 0.23)$
and hence $\lambda = 5.5$ (95% limits: 3.2-9.3)

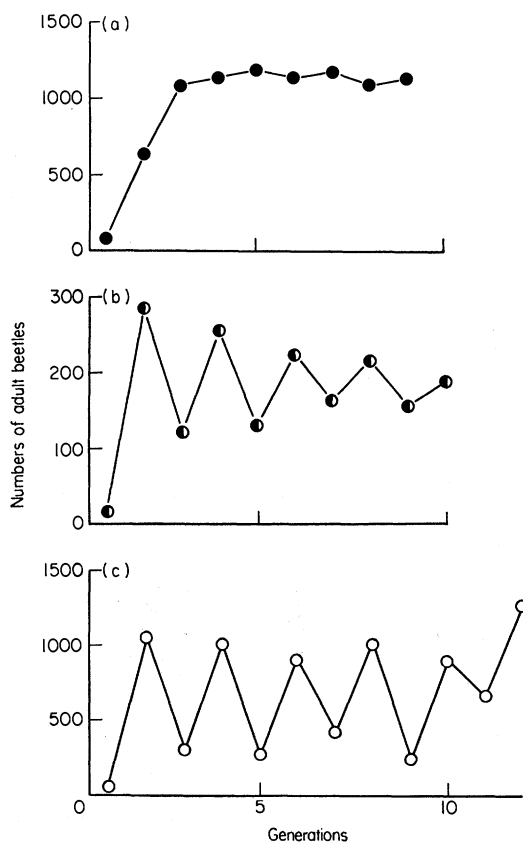


FIG. 3. Population changes in laboratory cultures of stored-product beetles. (a) *Callosobruchus chinensis* (after Fujii 1968); (b) *C. maculatus* (after Utida 1967) and (c) *C. maculatus* (after Fujii 1967).

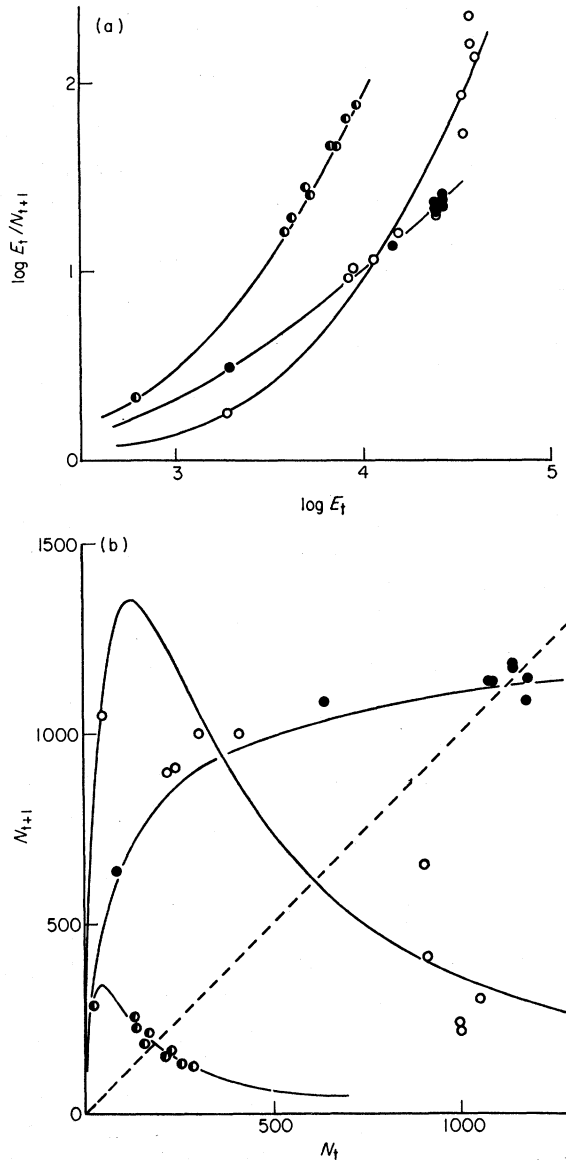


FIG. 4. (a) Density dependent relationships described by eqn (1) for the three populations in Fig. 3. (●) $a = 0.0013$, $\beta = 0.9$; (◐) $a = 0.0006$, $\beta = 2.2$; (○) $a = 0.0001$, $\beta = 2.7$. (b) Reproduction curves for the three populations in Fig. 3, described by eqn (1), using known values for a , β , and λ .

within the stable limit cycle region. This results from strong density dependence (larval competition as shown in Fig. 1(a), and adult migration) together with a high net rate of population increase. It is in accord with Harcourt's (1971) comments that *Leptinotarsa* populations fluctuate markedly with the tendency to 'over-compensate' from generation to generation.

The only other point that we single out is that for the grey larch bud moth (*Zeiraphera diniana* Gn.) in the Engadine. This is a graphic example where the single species model

does not describe the full dynamics of the population. *Zeiraphera* is well known as a species showing marked and regular oscillations with a period of eight generations (Baltensweiler 1968). Their cause is unknown; perhaps there is delayed feedback via the host food plant, or from some unknown insect parasitoids. However, in our analysis, *Zeiraphera* appears as a monotonically stable population. This is because the 'key factor' responsible for the oscillation is 'averaged out'. It is treated as a constant equal to its mean value in the calculation of λ from the fecundity per adult. That *Zeiraphera* is showing the weakest density dependence in Fig. 2 (point 1, closest to the origin) is in accord with the fact that 'predator-prey' limit cycles are most easily obtained when self-limitation on the prey is weak (May 1975b, pp. 92-3).

Laboratory experiments

The only true single-species systems are those contrived within the laboratory. They arise where a population (usually a stored product insect, a *Drosophila* species or a calyptrate fly) is cultured for several generations with a fixed amount of regularly renewed food in a constant environment. Such systems are therefore well described by equations such as (1), provided that generations remain more or less discrete. They provide valuable examples where the observed fluctuations are mainly the result of the internal dynamics and not 'imposed' by a variety of density independent mortalities. We shall examine in this section data from Fujii (1967) and Utida (1967) on the southern cowpea weevil (*Callosobruchus maculatus* (F.)), from Fujii (1968) on the azuki bean weevil (*C. chinensis* (F.)) and from Nicholson (1954) on the blowfly (*Lucilia cuprina* (Meig)), in each case obtaining estimates of β and λ which are plotted on Fig. 2.

Three examples of population fluctuation for *Callosobruchus* are shown in Fig. 3. They have been selected from several similar examples to show obvious (a) monotonic and (b) damped oscillations and (c) two-point limit cycle behaviour. For each experiment, estimates of the fertile eggs laid per adult beetle are given, which in these cases adequately represents λ since the only major mortality is due to the density dependent competition for food. We have, therefore, estimates of the total egg population in each generation ($E_t = \lambda N_t$) and hence of the total mortality ($\log E_t/N_{t+1}$). Figure 4(a) shows the resulting density dependent relationships, well described by eqn (2), and Fig. 4(b) re-expresses the data as a conventional reproduction curve (Moran 1950; Ricker 1954), in which the data are described by eqn (1). With estimates of β and λ , each experiment can be plotted on Fig. 2 (hollow circles). Both the monotonic and oscillatorily damped populations appear in the appropriate stability zones, while the limit cycling population (Fig. 3 (c)) lies on the margin of the limit cycle zone (but has much wider confidence limits on β).

As a final example, we select Nicholson's blowflies. Oster, Auslander & Allen (1976) have recently undertaken a detailed study of Nicholson's data, and have shown them to be well described by models whose dynamics lie in the chaotic region. We have estimated β from Nicholson's (1954) experiment where known numbers of newly hatched blowfly larvae were placed with 1 g of meat and the numbers of emerging adults recorded. The data are plotted in Fig. 7 of Hassell (1975) and yield a very high value of β ($\beta > 100$) consistent with the known 'scrambling' for resources of these larvae. This value will be independent of the amount of food per experiment, which should only alter the value for a . The estimate of λ is again taken as the average number of fertile eggs laid per adult ($\lambda = 55$). The resulting point on Fig. 2 lies comfortably within the region of chaos.

These four laboratory experiments give considerable support for eqn (1) and our method of analysis. The frequent occurrence of oscillatory behaviour in laboratory

cultures of insects is not surprising in view of their tendency to scramble for resources in close confinement ($\beta \rightarrow \infty$) and the general absence of large density independent mortalities ($\lambda \rightarrow \text{maximum fecundity per adult}$).

Range of fluctuations

Once outside the zones of exponential and oscillatory damping illustrated in Fig. 2, increasing values of β or λ lead to progressively more complex patterns of population behaviour. However, irrespective of the detailed dynamics, the population must lie between finite upper and lower bounds. Following the general recipe of May (1975a), it

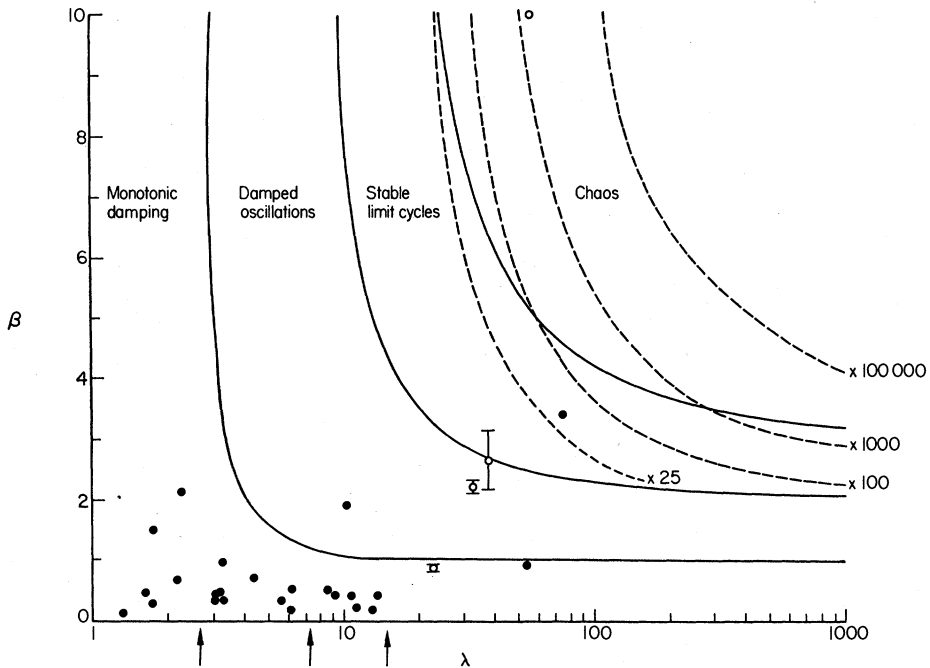


FIG. 5. As Fig. 2, but showing the boundaries for different values of the ratio N_{\max}/N_{\min} . Arrows mark the minimum values of λ for the different stability regions. (See text for further discussion.)

may be shown that, regardless of the initial population value, the ratio of the absolute maximum (N_{\max}) to the absolute minimum (N_{\min}) number of individuals in the population over a sufficiently long 'run' of data is given by

$$N_{\max}/N_{\min} = \lambda^{-1} (1 + \lambda(\beta - 1)^{\beta-1}/\beta^{\beta})^{\beta}. \quad (3)$$

Figure 5 shows the various ratios of N_{\max}/N_{\min} (broken lines) that have been calculated from eqn (3) within the limit cycle and chaotic regions. The dramatic increase in the ratio, as β and λ increase, is obvious.

Table 3 summarizes the limits within which a variety of natural populations have been observed to fluctuate, and it is notable that fluctuations of more than four orders of magnitude are very uncommon. The relationship of the examples in Table 3 to the boundaries in Fig. 5 is tenuous because the effect of additional density independent and delayed factors will inevitably increase the magnitude of fluctuations. All the same, the

Table 3. *The ratio of population maxima to minima (N_{\max}/N_{\min}) in a variety of field populations*

N_{\max}/N_{\min}	Generations or years observed	Species	Life-history stage	Reference
32000	60	Moth: <i>Bupalus piniarius</i> L.	Pupae	Varley (1949)
19000	18	Moth: <i>Zeiraphera diniana</i> Gn.	Larvae	Auer (1968)
20000	60	Moth: <i>Dendrolimus pini</i> (L.)	Hibernating larvae	Varley (1949)
790	11	Mollusc: <i>Clione limacina</i> (Phipps)	Summer adults	Williamson (1961)
690	14	Bug: <i>Saccarosydne</i> <i>saccharivora</i> (Westw.)	Larvae	Metcalfe (1972)
540	15	Moth: <i>Choristoneura</i> <i>fumiferana</i> (Clem.)	Larvae	Morris (1963)
460	60	Moth: <i>Panolis flammea</i> Schiff.	Pupae	Varley (1949)
400	21	Sawfly: <i>Diprion hercyniae</i> (Htg.)	Larvae	Neilson & Morris (1964)
340	13	Cockle: <i>Cardium edule</i> L.	One-year-olds	Hancock (1971)
320	60	Moth: <i>Hyloicus pinastris</i> L.	Pupae	Varley (1949)
240	5	Moth: <i>Callimorpha</i> <i>jacobaeae</i> L.	Adults	Dempster (1975)
170	12	Moth: <i>Acleris variana</i> Fern.	Larvae	Morris (1959)
160	10	Beetle: <i>Leptinotarsa</i> <i>decemlineata</i> (Say)	Adults	Harcourt (1971)
90	13	Cockle: <i>Cardium edule</i> L.	Two-year-olds	Hancock (1971)
88	16	Damselfly: <i>Enallagma</i> <i>cyathigerum</i> (Charp.)	Larvae	Macan (1974)
75	29	Moth: <i>Panaxia dominula</i> L.	Adults	Williamson (1972)
72	15	Parasitoid fly: <i>Cyzenis</i> <i>albicans</i> (Fall.)	Adults	Hassell (1969)
70	21	*Lemming: <i>Lemmus trimu-</i> <i>cronatus</i>	Summer adults	Schultz (1969)
64	18	Moth: <i>Operophtera brumata</i> (L.)	Larvae	Varley & Gradwell (1968)
60	11	Copepod: <i>Temora longi-</i> <i>cornia</i> (Mull.)	Summer population	Williamson (1961)
58	10	Leafhopper: <i>Nephotettix</i> <i>cincticeps</i> Uhler	Adults	Kiritani <i>et al.</i> (1970)
55	25	Wasp nests: <i>Vespula</i> spp.	Nests	Southwood (1967)
47	17	Damselfly: <i>Pyrrhosoma</i> <i>nymphula</i> (Sultz.)	Larvae	Macan (1974)
45	14	Moth: <i>Bupalus piniarius</i> L.	Larvae	Klomp (1966)
45	11	Arrow worm: <i>Sagitta</i> <i>elegans</i> Verrill	Adults	Williamson (1961)
40	14	*Bank-vole: <i>Clethrionomys</i> <i>glareolus</i> (Schreber)	Adults	Varley (1970)
40	13	Moth: <i>Orthosia cruda</i> (Schiff.)	Larvae	Varley & Gradwell (1963)
32	13	Moth: <i>Erannis leucoph-</i> <i>aearia</i> (Schiff.)	Larvae	Varley & Gradwell (1963)
29	6	Bug: <i>Nezara viridula</i> L.	Eggs	Kiritani <i>et al.</i> (1967)
26	6	Fly: <i>Oscinella frit</i> L.	Adults	Southwood & Jepson (1962)
24	15	Moth: <i>Erannis defoliaria</i> (Clerk)	Larvae	Ekanayake (1967)
23	9	Scale: <i>Parlatoria oleae</i> (Colvee)	Eggs	Huffaker & Kennett (1966)
22	10	Moth: <i>Erannis aurantiaaria</i> (Esp.)	Larvae	Ekanayake (1967)

Table 3 (*contd*)

N_{\max}/N_{\min}	Generations or years observed	Species	Life-history stage	Reference
20	14	Moth: <i>Hyphantria cunea</i> Drury	Larvae	Itô <i>et al.</i> (1969)
14	13	Moth: <i>Tortrix viridana</i> (L.)	Larvae	Varley & Gradwell (1963)
14	13	Moth: <i>Cosmia trapezina</i> (L.)	Larvae	Varley & Gradwell (1963)
12	18	*Great tit: <i>Parus major</i> L.	Breeding adults	Lack (1966)
11	14	Fly: <i>Chironomus anthracinus</i> Zett.	Larvae	Jonasson (1972)
11	9	Fly: <i>Erioischia brassicae</i> (Bouche)	Pupae	Mukerji (1971)
10	9	Beetle: <i>Philonthus decorus</i> Gr.	Adults	Varley (1970)
9	13	Moth: <i>Tortricodes</i> <i>tortricella</i> (Hb.)	Larvae	Varley & Gradwell (1963)
9	13	Moth: <i>Erannis progemma</i> (Hb.)	Larvae	Ekanayake (1967)
8	9	Fly: <i>Aedes aegypti</i> (L.)	Larvae	Southwood <i>et al.</i> (1972)
8	6	Fly: <i>Chaoborus flavicans</i> Meig.	Larvae	Jonasson (1972)
7	5	Beetle: <i>Phytodecta olivacea</i> (Forst.)	Adults	Richards & Waloff (1961)
5	13	Moth: <i>Eucosmaisertana</i> (Fab.)	Larvae	Varley & Gradwell (1963)
5	18	*Blue tit: <i>Parus caeruleus</i> L.	Breeding adults	Lack (1966)
5	53	*Cod: <i>Gadus callarias</i> L.	Adults	Gulland (1971)
5	13	*Great tit: <i>Parus major</i> L.	Breeding adults	Kluyver (1971)
4	36	*White stork: <i>Ciconia</i> <i>ciconia</i> L.	Breeding adults	Lack (1966)
3	13	*California vole: <i>Microtus californicus</i>	Summer adults	Lidicker (1973)
2	5	*Brook trout: <i>Salvelinus</i> <i>fontinalis</i>	One-year-fry	Hunt (1966)
2	16	*Pied flycatcher: <i>Ficedula</i> <i>hypoleuca</i> Pall.	Breeding adults	Lack (1966)
2	13	*Tawny owl: <i>Strix aluco</i> L.	Breeding adults	Southern (1970)
2	19	*Heron: <i>Ardea cinerea</i> L.	Breeding adults	Lack (1966)
<10	14	*22 spp. of British birds	Adults	Ginn (1969)

* These vertebrate populations, in particular, are not appropriately described by model (1) because they do not have discrete, non-overlapping generations. They have been included in the table to make it representative of a wider range of available data.

boundaries in Fig. 5 show that on the grounds of observed fluctuations alone the chaotic region is unlikely to be attained by natural populations.

Indeed, evolutionary considerations suggest that extreme fluctuations are unlikely because the populations would need to be very abundant or vagile to persist.

Estimates of λ

Figure 5 also usefully indicates the minimum values of the net rate of population increase, λ , for the various stability regions. Thus, damped oscillations are only possible if $\lambda > 2.7$, stable limit cycles in $\lambda > 7.4$ and chaos if $\lambda > 15$. These minimum values of λ for the different stability regions (which only apply in the limit $\beta \rightarrow \infty$) are marked by the arrows along the λ -axis in Fig. 5. As β decreases, so the lowest values of λ for a particular stability region increase until when $\beta < 3$, chaos is no longer possible for any sensible

rate of increase. Similarly, stable limit cycles are not possible when $\beta < 2$ and not even damped oscillations if $\beta < 1$.

An alternative way of framing these remarks is to take the simpler population model

$$N_{t+1} = \lambda N_t \exp(-\alpha N_t) \quad (4)$$

which, in contrast to the three-parameter model (1), involves only two parameters, λ and α . This model has been extensively used as a specific example in general discussions of the way stable points, stable cycles, or chaos arise (e.g. May 1974; May & Oster 1976). Its stability behaviour is determined solely by the single parameter λ (the population's rate of increase). Although the simpler model (4) gives a cruder fit to the population data than does the more detailed model (1), it is instructive to compare the stability behaviour of various populations as predicted by the two models. This comparison is easily made by noting that the model (4) is a special case of the model (1), namely the limit $\beta \rightarrow \infty$, $a \rightarrow 0$, keeping $\beta a = \text{constant} = \alpha$. Thus the stability behaviour of model (4) depends only on the λ -value for the population, and the stability boundaries (obtained as the limit $\beta \rightarrow \infty$ in Fig. 5) are as discussed in the preceding paragraph and marked by the arrows on the λ -axis in Fig. 5.

From Fig. 5, we can see that realistic λ -values will, of themselves, preclude almost all natural populations from the regime of chaos and most from the region of cycles, regardless of the value of β . Considering both natural and laboratory populations, we see that the more refined model (1) predicts twenty-six populations to have a stable point (twenty-three of them monotonically damped), one to have stable cycles and one to be chaotic. The cruder model (4) gives fifteen with stable points (six of them monotonically damped), seven with stable cycles and six in the chaotic regime. A major discrepancy lies in the laboratory populations with their high λ -values, where there are three populations which are described as stable points by model (1) and as chaotic by model (4).

We must remember that λ is the net rate of increase after all density independent mortalities have been accounted for. The role of density independent mortality in reducing a high maximum fecundity to a relatively low net rate of increase, λ , has already been illustrated by the winter moth example in Table 2. An extreme case is for the insect parasitoid, *Cyzenis albicans* (Fall.) (point 9, Fig. 2), where a fecundity of about 2000 eggs per female is possible but λ is only 7.4 due to a very high density independent egg mortality.

In the absence of any quantitative measure of the sources and types of density independent mortality acting on a particular population, it will clearly be extremely misleading to argue about possible λ -values from a knowledge based only on maximum fecundity. One possible group of examples from many will further emphasize this point. Many freshwater zooplankton populations have very high maximum fecundities per generation, of the order of 500 to 2000 in *Daphnia* (Hall 1964; Arnold 1971), 250 in *Simocephalus* (Murugan & Sivaramakrishnan 1973) and 100 in *Cyclops* (Elbourn 1966). At the same time, successive generations fluctuate between rather wide limits and, because zooplankton populations are extremely difficult or even impossible to census in a manner that is at all appropriate for a life-table analysis, we cannot prove that they do not provide examples of higher order limit cycles or even chaos. In reality, however, such behaviour again appears to be rather unlikely. Realized rates of increase in field populations of *Cyclops* were only of the order of three per generation (Elbourn 1966), whilst *Daphnia* populations in the field rarely experience periods of maximum daily instantaneous rates of increase, r , ($\lambda = \exp(r)$) greater than 0.1 to 0.2 for more than a few days ($t = 20$),

and certainly for less than one generation (Hall 1964; George & Edwards 1974). We suspect that realized λ -values in zooplankton are, on average, considerably less than a cursory examination of maximum potential fecundity data would suggest. Similar remarks almost certainly apply to other organisms with high maximum potential fecundities per generation, although we make this remark more in a spirit of provocation and ignorance than in the light of any sound biological information.

DISCUSSION

By focusing on one general model for the growth of a single-species population with non-overlapping generation (namely, eqn (1)) and then using this model to estimate appropriate parameter values for real populations, we conclude that some of the types of dynamical behaviour that are possible in theory, in fact, rarely occur in real, single-species populations. Figure 2 bears this out. Most of the populations show monotonic damping back to an equilibrium following a disturbance, with only the occasional example of oscillatory damping or some sort of low-order limit cycle.

The exception to this generalization, in the data we have surveyed, is itself illuminating. Nicholson's blowflies appear to lie in the chaotic regime, a result substantiated in much more detail by Oster *et al.* (1976). But this is a laboratory population, freed from many of the mortality factors that occur in the outside world. Consequently, its net growth rate is relatively high and the population is able to increase rapidly from low densities; the subsequent high population densities then exhibit dramatic crashes due to the tendency to 'scramble' for resources. That is, the laboratory situation may make for exaggeratedly non-linear behaviour. Most of the other points in or near the cyclic regime in Fig. 2 also come from laboratory populations, the one notable exception being the Colorado potato beetle. Thus on the present evidence we conclude that high-order limit cycles and chaos appear to be relatively rare phenomena in naturally occurring single-species populations.

In interpreting this conclusion, a long list of reservations and qualifications must be kept in mind. Some of these are as follows.

First, the conclusion may depend sensitively on the model. This point was discussed earlier. The fact that the conclusions reached for the three parameter model (1) are broadly in accord with those reached using the much cruder two-parameter model (4) (i.e. where stability depends only on the population growth rate, λ), suggests that they are robust to the choice of model.

Second, the conclusions apply only to single-species populations in which the density dependence is viewed as some process arising from within the population. We have excluded any explicit reference to interactions with other populations (either as food, competitors, parasites or predators), although these may be present implicitly as factors contributing to the density dependent term $\beta \log(1 + aN_i)$ in eqn (2). In at least one case (for the larch bud moth, point 1 on Fig. 2), this gives a misleading impression of the dynamics of a naturally occurring population, as discussed earlier.

Third, it could be that the data on natural populations that we have surveyed is biased towards studies on less variable populations. Such a bias would lead to our underestimating the prevalence of high-order limit cycles and chaos. There is no way that we can prove that this is not the case, but it seems unlikely.

Fourth, our models apply directly only to the restricted range of organisms with completely discrete generations. However, even in the opposite extreme of continuously overlapping generations, so that the population is modelled by a differential equation,

there can arise limit cycles (and, possibly, chaotic dynamics if the non-linearities are complicated enough) provided that the density dependent mechanisms embody sufficiently long time-delays. Such analogies between difference equations and differential equations with time-delays are discussed at length by May *et al.* (1974), and lead us to believe that the difference equations discussed in this paper are likely to characterize a wide range of models.

Fifth, our model takes no explicit account of migration and dispersal, and may thereby give a misleading account of some natural populations.

Finally, we emphasize that the complete range of behaviour, from stable points, through stable cycles to chaos, also arises in interactions with two competitors (May 1974; Hassell & Comins 1976) or predators and prey (Beddington, Free & Lawton 1975). Indeed, as reviewed by May & Oster (1976), there are grounds for thinking that chaotic dynamics may arise more readily in multi-species situations. Thus, morals drawn from single-species studies must be treated with caution.

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SUMMARY

(1) A variety of data on field and laboratory populations is reviewed in which there is little or no overlap between generations. These data are then fitted to a simple, non-linear, density dependent population model.

(2) A rich spectrum of dynamical behaviour is possible in such a non-linear model (ranging from a stable equilibrium point, through stable cycles, to apparently chaotic population fluctuations). In the particular model discussed, these stability properties hinge upon two parameters. These have been estimated for a variety of insect populations enabling us to compare the dynamical behaviour of real populations with that which is theoretically possible.

(3) We find the majority of populations show a monotonic return to a stable equilibrium point following a disturbance, with relatively few examples of oscillatory damping or low-order limit cycles.

(4) Examples of stable cyclic behaviour, or of chaotic fluctuations, are mostly found in laboratory populations. In such cases, the absence of many natural mortality factors, or of dispersal, may tend to exaggerate non-linear aspects of the dynamics.

(5) The observed range of fluctuations in various populations is tabulated. These are discussed in relation to the predicted ranges of fluctuation where limit cycles or chaos occur. The conclusion supports that of (3) above; namely that most natural populations will tend to return to a stable equilibrium point following a disturbance.

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