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POPULATION DYNAMICS: MODELS BASED ON INDIVIDUAL GROWTH, RESOURCE ALLOCATION AND COMPETITIVE ETHOLOGY

by

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1 GENERAL INTRODUCTION

This paper presents general models for population dynamics that are similar in structure and concept to both the familiar Leslie matrix models and matrix models of energy flow. The model initially is developed into a density-dependent model not by the use of mathematical formulae but by the use of two simple algorithms which describe, albeit crudely, competitive ethological interactions for limited food resources and the effects of these on the subsequent growth of the contestants. Example simulations are shown, using hypothetical data, for:- unrestrained population growth; constrained population growth in a uniform temporal environment; constrained population growth in a seasonally varying environment. These simulations are shown for two extreme types of competition, 'SCRAMBLE' and 'CONTEST'. These simulations verify (sensu Jeffers 1978) that the general behaviour of the models is ecologically reasonable, indicating that there are no fundamental errors in their assumptions or formulation. I have, unfortunately, so far been unable to attempt validation (sensu Jeffers) of the model due to the lack of a suitable and simple data-set. Accordingly a major purpose of this paper is to present the models to field ecologists and ethologists for their assessments of the reasonability of the models and, hopefully, to establish whether there are any pre-existing data sets that would permit their proper testing.

In the absence of suitable data for validation the paper goes on to briefly outline a number of ways in which the simple initial models could be expanded to address more complex situations and secondly to indicate by what means suitable data sets could be most readily collected.

These models are not intended as prescriptions to solve, of themselves, problems in population ecology but rather, following the lead of Lomnicki (1978, 1980), to question the relevance of some current mathematical formulations and to suggest an alternative approach by incorporating into population models important and fundamental aspects of natural history, life-history and ethology.

2 HISTORICAL BACKGROUND

2.1 Classical mathematical models

Population dynamics dates back at least to the time of Malthus (1766-1834) and, in its classical form, is concerned with the numbers, and changes in numbers, of populations of a species. It has fairly deep roots in human demography and a fair history of mathematical descriptions. The earliest of these take simple forms, eg:

$$dN/dt = r.N \tag{2.1}$$

$$dN/dt = r.N \, \frac{K-N}{K} \tag{2.2}$$

or, in difference equation form

$$N_{t+1} = N_t + r.N_t \, \frac{K-N_t}{K} \tag{2.3}$$

and its more elaborate derivatives

$$N = N \, (1 + r \, (1 - N/K)) \tag{2.4}$$

$$N = N \exp \, (r \, (1 - N/K)) \tag{2.5}$$

$$N = \lambda \, N \, (1 + \alpha \, N)^{-B} \tag{2.6}$$

$$\left.\begin{array}{ll} N = \lambda \, N^{1-b}; & \text{for } N > E \\ N = \lambda \, N \; ; & \text{for } N < E \end{array}\right\} \tag{2.7}$$

These equations have stood the test of time in theoretical biology, but have not been widely used in detailed studies of populations by field ecologists. It is reasonable to suggest that this dichotomy of approval is due to the fact that, while the above formula (2.2 → 2.7) are sufficiently complex to give a reasonable fit to most likely curves that show changes of numbers with time their parameters are not readily interpretable in a detailed ecological sense and they are founded on assumptions that field ecologists recognise to be very shakey.

A basic assumption of such simplistic formulations, usually left as implicit and not stated explicitly is that all individuals in the population are absolutely identical in terms of age, sex and phenotype (remember phenotype = genotype * environmental influences) or, at least, that any differences between individuals in respect of these aspects are trivial with regard to population dynamics. More complex population models recognise the importance of age and sex differences and population genetics has a wide range of models showing how genetic factors affecting aspects pertinent to population ecology could maintain genetic polymorphisms. Theoreticians often claim that there is little evidence from field ecology that such aspects are important in population dynamics, but such statements ignore (i) the growing body of evidence which there is (often from disciplines with which theoreticians are not familiar); (ii) the mathematical training of previous theoreticians who have trained the small minority of today's ecologists who use detailed numerical methods; (iii) the complexity of designing experiments to show such effects from field data and, finally, we might include (iv) the incorporation of all these factors (or indicators of them such as family history for genetic influences) into the actuarial tables of life insurance companies.

2.2 Leslie matrix models

One of the best known forms for structured population models is the matrix model due to Leslie (1945) and used to predict age-structure. The developments of this family of models ('Leslie matrix models') is usefully reviewed by Usher (1972), who indicates how various workers have incorporated sexual differences, and complex life stages and so on.

As the models put forward in this paper are similar both in concept and mathematical structure to Leslie matrix models I propose to describe Leslie models here in adequate detail for readers unfamiliar with them. Anyone desiring further details should consult Usher (1972) and Jeffers (1978).

The Leslie model envisages a population separated into age classes (the classes representing identical time periods/age differences in the simplest forms), and the numbers of animals in each age class are represented by a column vector of numbers, as shown in column three of Diagram 1a opposite. The model works in discrete units of time (the class period), so, given the numbers in column 3 of diagram 1a, we could obtain the numbers in the next period of time by multiplying them by the given survival rates and adding to them the product of themselves and their corresponding *per capita* fecundities (columns 4 and 5 of Diagram 1a).

It is mathematically and computationally convenient to write such data in the form of two matrices, as shown in Diagram 1b. The rules of matrix multiplication (column vector answer element) = sum of (each element of a row x each element of a column), repeated for all elements and every row/column give an identical answer to that described above in relation to Diagram 1a; readers unfamiliar with matrix operations may care to verify this.

In matrix notation this operation can be written:

$$\underline{a}_{t+1} = \underline{A} \times \underline{a}_t . \qquad (2.8)$$

The square matrix $\underline{A}$ is referred to as a transition matrix as it represents the 'probabilities' that 'individuals' will 'move' from one class to another. Thus, as indicated in Diagram 1c, the terms on the sub-diagonal represent 'survival', as each animal in a class becomes older in the next unit of time and must hence move to the next class. Similarly, the top row of the matrix represents *per capita* fecundity from each of the age classes to the youngest class, into which animals are 'born'. All other elements of the square matrix must be zeros, due to the model's definition.

DIAGRAM 1: Leslie Matrix Model

Diagram to show how the survival and fecundity terms of a simple life-table (1a) can be written in terms of matrix algebra, (1b) to provide a discrete-time population model and illustrating (1c) how the structure of the transition matrix can be interpreted as survival and fecundity terms.

1a

Age Class	Age	No.s	Survival	Births
i	0-4	48	.333	0
ii	4-8	8	.500	9
iii	4-12	2	0.000	12

1b

$$\begin{array}{ccccccc} \text{Transition matrix} & & \text{Age structure } t=0 & & \text{Calculation} & & \text{Age structure } t=1 \\ \begin{pmatrix} 0 & 9 & 12 \\ .333 & 0 & 0 \\ 0 & .5 & 0 \end{pmatrix} & \times & \begin{pmatrix} 48 \\ 8 \\ 2 \end{pmatrix} & = & \begin{matrix} 48 \times 0 + 8 \times 9 + 2 \times 12 \\ 48 \times .33 + 8 \times 0 + 2 \times 0 \\ 48 \times 0 + 8 \times .5 + 2 \times 0 \end{matrix} & \begin{matrix} = \\ = \\ = \end{matrix} & \begin{pmatrix} 96 \\ 16 \\ 4 \end{pmatrix} \end{array}$$

1c

Transition matrix, $\underline{A}$ = Survival, $\underline{P}$ + Fecundity, $\underline{F}$

$$\begin{array}{cc|ccc} & & \multicolumn{3}{c}{\text{Class From}} \\ & & \text{i} & \text{ii} & \text{iii} \\ \hline & \text{i} & 0 & 9 & 12 \\ \text{CLASS} & \text{ii} & .333 & 0 & 0 \\ \text{TO} & \text{iii} & 0 & .5 & 0 \end{array} = \begin{array}{c} \text{Class From} \\ \begin{array}{ccc} \text{i} & \text{ii} & \text{iii} \end{array} \\ \begin{pmatrix} 0 & 0 & 0 \\ .333 & 0 & 0 \\ 0 & .5 & 0 \end{pmatrix} \end{array} + \begin{array}{c} \text{Class From} \\ \begin{array}{ccc} \text{i} & \text{ii} & \text{iii} \end{array} \\ \begin{pmatrix} 0 & 9 & 12 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \end{array}$$

The matrix structure therefore represents a convenient and powerful summary of the data shown in Diagram 1a, but, more importantly, two algebraic properties of the square matrix, its eigenvalue and eigenvector (see, eg. Dorf 1969, for mathematical definitions of these) can be calculated simply by readily available computer algorithms, and are of direct relevance to population dynamics. For example in the matrix shown in Diagram 1 (whose values are taken from Williamson 1967), there is a dominant eigenvalue of 2.0 and an associated eigenvector of (24, 4, 1). It can be readily shown that the dominant eigenvalue, λ, corresponds to the rate of population increase (note that the values for time = t+1 in Diagram 2a are all 2.0 x those for time = t) and is related to the intrinsic rate of population increase, r, by the equation:

$$r = \log_e \lambda \qquad (2.9)$$

The eigenvector corresponding to λ gives the (relative) stable age structure, which for this example, is maintained at ratios of 24:4:1 at all time periods.

It should be stressed here that this model closely approximates the calculus form for exponential population growth (equation 2.1) (which could be re-written: $N_t = N_o e^{rto}$; 2.10). It is possible, but complex, to introduce density-dependent functions into the elements of matrix $\underline{A}$ to produce models of limited populations, similar to those described, overall, by equations 2.2 → 2.7. Such elaborations are mathematically complex: summaries of such attempts are given in Jeffers (1978) and Usher (1972) and two useful examples are Usher (1969) and Beddington (1975).

We should note finally two limitations of Leslie population matrices. First, they are really deterministic, despite incorporating probability values; and second, the fecundities are averages for the whole class. This means that if the class contained, for example, 100 animals of whom only 10 bred, rearing a total of 50 offspring, the fecundity term of the Leslie matrix would be 50/100 = 0.50. To my mind this obscures an extremely important fact: 10% of this age class bred very successfully before the majority of that age class were able to. I suggest that such situations are not rare (though this example is deliberately extreme), that they may have important genetic consequences and that they may be fundamental to the population's ability to survive in a varying environment. Accordingly, I believe it is vital to understand what aspects of such 'early breeders' allow them to breed unusually early and would like to see structures for population models that help elucidate these aspects. I hope that the models developed in this paper go some way toward achieving this. This single class example was used for the sake of clarity but it should be realised that it applies to all age class of breeders in practice.

2.3 Individual differences, resources and ethology

The deficiencies of classical population models which I elaborated above are not novel, but have been levelled by field ecologists for some time. Until recently however, there have been no suggestions as to how these deficiencies might be remedied. I believe the recent papers by Lomnicki (1978, 1980) give a key to how this may be achieved and certainly throw a refreshing and stimulating light on a rather stale controversy. The ideas put forward by Lomnicki (loc. cit.) are fundamental to my own concepts (which were greatly enlightened by his papers) and underly much of the structure of the models presented later. Lomnicki's papers are, per force rather mathematical in nature, but easy to follow in principle and aimed at highlighting inadequancies of **assumptions** in previous population models. I was encouraged to find during the course of a brief correspondence that Professor Lomnicki continually re-emphasised the importance of natural history and ethology to the development of realistic population models: regrettably, many theoreticians in population ecology regard these as no more than awkward irrelevancies, assuming that they are actually aware of them. I would strongly recommend readers to refer to Lomnicki's papers, but will briefly outline below the major points, particularly those most pertinent here.

Lomnicki emphasises that most models of population dynamics ignore:

i. life histories and natural history
ii. fundamental and critical aspects of ethology such as competition and territorial behaviour
iii. habitat heterogeneity
iv. the problem of why, and particularly when, animals disperse.

Taking the latter point as an illustration, it is evident that most population models and many field ecologists either ignore immigration and emigration (from/to the 'study area') or assume it to be constant, which is much the same as ignoring it. Lomnicki (1978) shows that, given a population with a social hierarchy, differences between individuals in resource allocation and habitat heterogeneity, population regulation may actually be <u>achieved</u> by emigration. The proposed mechanism is that, in relation to a defined study area emigration is density dependent and, as mortality due to emigration will not be observed within the study area, data from such studies would not show density dependent mortality although the population is <u>regulated</u> by density dependent emigration.

Lomnicki's later paper (1980) develops a population model in which the regulation is based on differential allocation of resources to individuals in a social hierarchy, with consequent individual differences in fecundity and survival prospects and allowing partitioning of resources between growth and reproduction.

2.4 Utilisation of field data

2.4.1 Inadequacy of 'numbers' for describing a population

I have suggested above that the various classical equations (2.1-2.7) above are capable of producing a wide variety of curves and that, given likely estimation errors of field data, a time series of N with t may be equally accurately approximated by more than one of these equations. How then could one decide which, if any, of these equations give the 'best' fit?

Now let us examine the problem from a different aspect. The data for such models come from field studies, often of marked individuals, and require the use of the following information per individual:

No age structure	Age structure
time of birth	time of birth
estimated age at death	estimated age at death
lifetime productivity	productivity at ages $b_1, b_2 \ldots b_n$

This is often only a small proportion of the information the investigator will collect: in vertebrate studies at least the marked individuals will often be weighed and measured at each capture. Regrettably, such information is rarely incorporated into studies of population dynamics. Too often the literature reveals the following approach:-

Bloggs, B.F. & A. Twitson, 1982. A population dynamics model of the long-haired vole (*Microtus whatsitae*) at Over-Puddle marsh, Blankshire, 1979-1981. J. Misappl. Maths. 13, 1029-1136.

Bloggs, B.F. & S. Ation, 1983. Weight changes in a population of the long-haired vole (*Microtus whatsitae*) at Over-Puddle marsh, Blankshire in relation to the harsh winter of 1930/81. J. Wildl. Nutrition 4, 7-63.

In such instances we might well find that the earlier paper used a model designed to represent a stable population in a uniform environment, despite "Dr. Bloggs" recognition of the catastrophic mortality due to the severe winter and omitting the data which he could have extracted on 'breeding condition in relation to spring weight' the following season.

In short, common sense suggests that realistic models of the complex dynamics of natural populations will require much more information than is used to construct classical models and that investigators would be wise to strive to incorporate those aspects of their populations' interactions which they know to have important consequences to survival, mating success, fecundity, dispersal and the like even if such knowledge is culled from widely separated biological disciplines.

2.4.2 Habitat heterogeneity

I referred above to Lomnicki's demonstration that emigration and habitat heterogeneity may be fundamental to population dynamics and have mentioned elsewhere (Macdonald, Bunce & Bacon 1981) that studies of population dynamics are usually undertaken at sites chosen largely for convenience rather than as being representative of typical areas. Indeed, although a variety of techniques are available for habitat description, these are rarely used by population biologists to sub-divide their study areas. In short, habitat heterogeneity is likely to be fundamental to important aspects of population dynamics and, if this proves to be the case, population models that can readily incorporate such differences will be needed.

2.4.3 Population genetics

There is overwhelming evidence from population genetics that polymorphism is widespread and that (artificial) selection can rapidly alter characters important in population dynamics (see Gale 1980 for a readable review). The evidence that such polymorphisms do have appreciable effects in natural populations is presently sparse (see above) but taken in concert with the wealth of basic data from population genetics is sufficient to suggest that detailed mechanisms of population dynamics may be affected by, and themselves affect, gene frequencies.

2.5 Outlook

I have summarised above shortcomings, which I believe to be serious, in most present formulations for population dynamics models and indicated that I consider the suggestions of Lomnicki (1978, 1980) to offer an instructive way out of the present impasse. In the following sections I discuss model structures based on tenets very similar to Lomnicki's. These structures may be applicable to a wide range of field studies. I do not pretend to offer prescriptions to solve a host of problems in population ecology (although the models I develop here may be directly applicable to simple situations and some species) but hope rather to suggest concepts and model structures that might be developed to permit solution of many diverse population processes. I recognise that the formulations I suggest will still seem over-simple to field ethologists and are probably mathematically unattractive to biometricians. I hope however that in considering the shortcomings of my suggestions scientists from both disciplines may find them a useful focus for discussion and I hope particularly that they may provide some common ground on which researchers from both extremes can readily enlighten each other.

2.6 Summary

I conclude above that present models of population dynamics seriously omit to account for biological variation, which may be considered to have three aspects:

i. phenotypic variation among individual animals, due to genetic and environmental influences

ii. variation in the habitats that populations occupy

iii. temporal variations caused by differing population responses to environmental factors, such as weather, which vary from year to year and interact with the 'dynamics'.

3 POPULATION MODELS: GROWTH AND COMPETITION

3.1 Concept and model structure

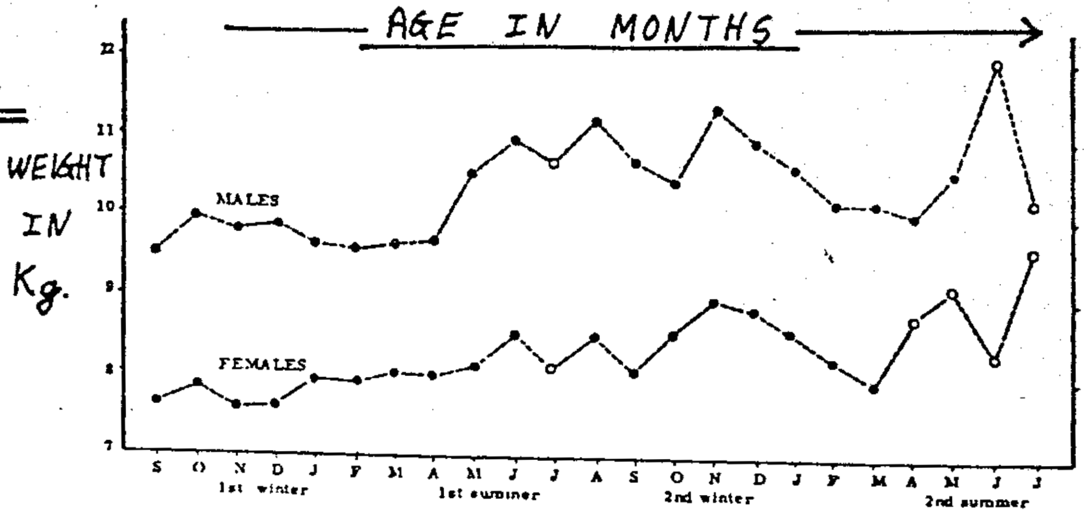
A possible structure for population models based on ecological rather than mathematical principles occurred to me whilst considering some data on weight changes in Mute swans (Cygnus olor) shortly after reading Lomnicki's paper (1980). The model described in the following sections is more applicable to 'long lived' organisms, having several reproductive periods per lifetime than to discrete generation populations or 'short lived' organisms having few reproductive periods per lifetime.

A basic tenet of the model is that 'weight' or 'condition' and 'social dominance' are positively correlated for the population being modelled. I believe, as does Lomnicki 1980, that this assumption holds reasonably for many animal populations and, particularly, that it is true and appropriate for the Mute swan populations I was initially concerned with. It is likely to be true for Mute swans because: (i) they engage in violent physical combat to settle disputes, (ii) weight increases with age, Diagram 2a, (iii) age and social dominance are inversely correlated (rank 1 = highest dominance), Diagram 2b; hence (iv)-(i), (ii) and (iii) imply that weight will be correlated to social dominance, as shown in Diagram 2c.

I note in passing that the main tenet of these models is diametrically opposed to the assumptions of such techniques as 'length-frequency' data analysis for studying population processes. These methods (eg. Pauly & David 1980) assume that size (length, weight) is completely determined by growth rate, such that any animals of the same size are assumed to have precisely the same ages. While such techniques may provide a useful first crude assessment of population growth characteristics (eg. for fisheries biologists, Pauly & David loc. cit.) such approaches seem quite unrealistic. If such length-frequency models do apply to some real species in any detail then the 'Condition' models described in this paper would most certainly not apply to those same species!

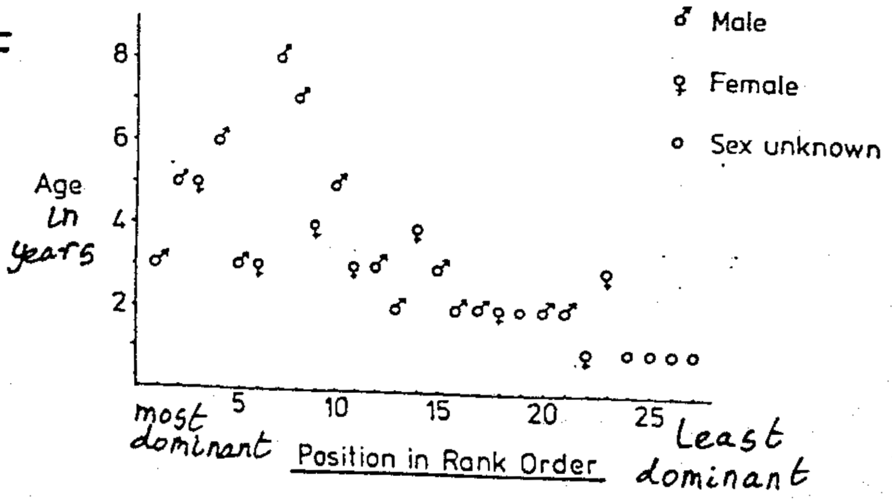
Diagram 2. Relationships between Age, Weight and Social Dominance in Mute Swans. Figure 1a, taken from Reynolds 1972, shows weight increases with age for both males and females. Figure 1b, from Lesselles 1975, shows Social Dominance in relation to Age. Hence we may deduce, Figure 1c, that Weight and Social Dominance will be related.

Dia. 2a



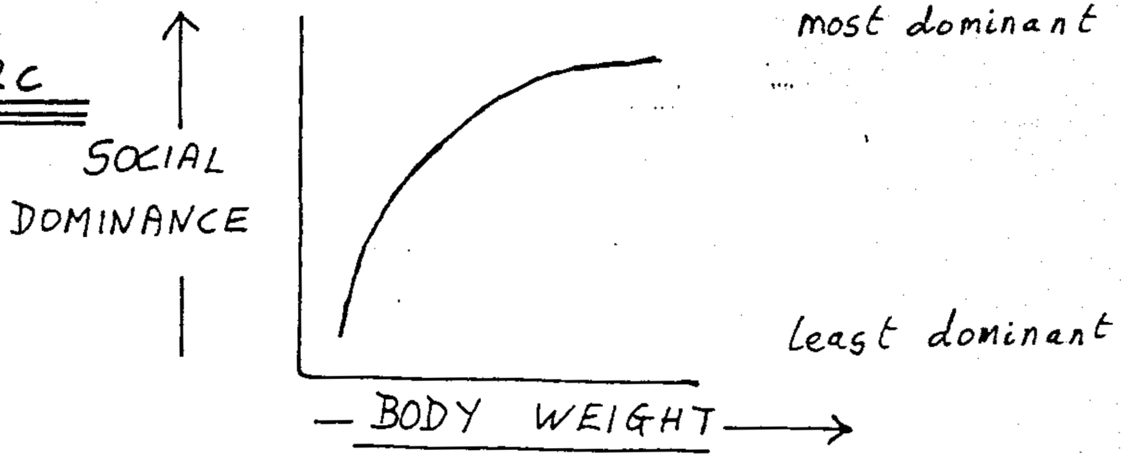
Age Plotted Against Position in the Rank Order.

Dia. 2b



HENCE

Dia. 2c



While the models described here have been developed with such particularly suitable species in mind it is likely however that they would hold for a much wider range of species, albeit with less exactitude. The reader is encouraged to consider to what extent such models might adequately reflect the dynamics of populations of species with which he is particularly familiar in the field. In doing so he should remember that, while the examples I use here refer mainly to birds and mammals, there are however long lived, slow growing invertebrate species to which the models might equally well apply. He should also seriously consider the time scales involved: while the food reserves accumulated by a large animal may last it for some time, for example one to two months for Mute swans (Andersen-Harild 1980) the maximum food reserves that may be accumulated by a small passerine, such as a Bullfinch, will only keep the passerine alive for about one and half days (Newton 1972).

3.2 Model formulation

We concluded above that we were interested in the partitioning of food, or energy, resources between individuals and that within individuals we are also interested in the partition between (i) growth and maintenance and (ii) reproduction.

We shall assume that individuals that have greater sizes or social dominances will have different breeding potential and, for simplicity, we will further assume that body weight is a good index of social dominance and breeding potential.

Consider therefore the possible changes that could occur over a specified period of time to ANY individual of known weight at the start of the period. During the period it will be searching for food, eating food, converting the food into energy, body mass or reproductive mass, and it will be exposed to various risks of death. We might summarise the eventual possible outcomes, for itself, as:

I: i. Death
   ii. Nett loss of weight
   iii. Weight maintained
   iv. Net gain of weight

While II: it might have reproduced, with varying degrees of success. Some reproductive success could, in theory, be expected for all outcomes I: i.-iv. above. On average, we would expect however, that the 'heavier' animals would reproduce more effectively.

We could envisage characteristic probabilities of each outcome I: i-iv for each weight class, W_i, and also characteristic fecundities. The most convenient way in which to summarise such changes would seem to be in the form of a compartment model that is very similar in structure and concept to a Leslie Matrix model. The important difference however is that the dimension(s) of the matrix represent Weight (or condition or social dominance) classes, not age classes. In practice such assignment would be easy for some species but problematical for others. For example the daily weight fluctuations of individual Bullfinches may exceed the variations of the population mean over a whole year (Newton 1972), and in such instances obtaining weights at standardised times would be difficult, occasionally even impractical perhaps.

The process of setting up such a matrix is shown in Table 1, but first it is necessary to formalise the model a little more:

Assume a population of animals can be separated into C classes on the basis of condition/weight/social dominance. For each class, C_i, there are characteristic probabilities that an individual in the class at the start of a period of time will suffer one of the following fates by the end of the period.

i. it will lose weight, and become a member of the next lower class. For the case of individuals already in the lowest class, these are assumed to drop below a critical threshold and starve to death during the period
ii. it maintains its weight, and remains in the same class at the end of the period
iii. it gains weight, and enters the next highest class at the end of the period
iv. it dies from density independent causes.

These possibilities are illustrated in Table 1a. The model, as here defined assumes a time period sufficiently short that only one change in class can be achieved per interval. More complex conditions could, however, clearly be coped with.

Similarly, for each weight class C_i there is a characteristic set of fecundities such that, during the time period, the per capita production of offspring into the various weight classes will be F_{ij}, where:

i = 1 to C and denotes parental class
j = 1 to C and denotes offspring class

as illustrated in Table 1b.

These survival and fecundity values may be written in matrix form, as illustrated in Table 1c.

We note the following important differences from the familiar Leslie Matrix formulation:

Dynamics. The model permits much more complex dynamics, allowing considerable flux around the various condition classes. The usual form of a Leslie matrix, although based on some probability values, enforces a completely deterministic progression from one class to another (an exception is Usher's model for the growth, which has probabilities for (a) growing, (b) staying the same size). The

TABLE 1

The table starts (1a) by showing how individuals in classes i–v might be considered to: Starve, S; Loose Weight, L; Maintain Weight, M; Gain Weight, G; Die, D. Part (1b) shows how fecundity values could be ascribed to each class. Part (1c) illustrates the structure of a matrix corresponding to the changes S, L, M, G, D, f and ff listed in parts (1a and 1b), while part (1d) illustrates the structure of the matrix by substituting numerical values for the variables. These values (1d) are used later in the paper as EXAMPLE DATA SET 2. EXAMPLE DATA SET 1 has no fecundity term on row 2 (ie. ff v = $\underline{P}_{2,5}$ = 0.00) and the fecundity term of class (v) into class (i) is 5.5 not 4.5 (ie. fv = $\underline{P}_{1,5}$ = 5.5). See also Table 4.

1a

Category of 'Weight' change etc.	Starting classes of the individuals				
	i	ii	iii	iv	v
Starve	Li = S	-	-	-	-
Loose Weight	-	Lii	Liii	Liv	Lv
Maintain Weight	Mi	Mii	Miii	Miv	Mv
Gain Weight	Gi	Gii	Giii	Giv	-
DIE (density) (independent)	Di	Dii	Diii	Div	Dv

1b

Fecundity		Starting class of parents				
		i	ii	iii	iv	v
Offspring reared into classes:-	i	-	-	fiii	fiv	fv
	ii	-	-		ffiv	ffv
	iii	-	-	-	-	

1c

The Matrix structure		'FROM' CLASS				
		i	ii	iii	iv	v
'TO' CLASS	i	Mi	Lii	0	fiv	fv
	ii	Gi	Mii	Liii	0	ffv
	iii	0	Gii	Miii	Liv	0
	iv	0	0	Giii	Miv	Lv
	v	0	0		Giv	Mv
	∴ DIE	Di + Li	Dii	Diii	Div	Dv

1d

Example values for P matrix		i	ii	iii	iv	v
	i	0.50	0.14	0.00	4.5	4.0
	ii	0.10	0.58	0.10	0.0	1.0
	iii	0.00	0.13	0.64	0.10	0.00
	iv	0.00	0.00	0.16	0.67	0.10
	v	0.00	0.00	0.00	0.18	0.85
	∴ DIE	0.40	0.15	0.10	0.05	0.05

condition model (as currently described) although deterministic in the form of its output nonetheless encapsulates several different 'routes' to and from each class; the characteristic time periods for these routes will, ecologically, be reflected in the age distributions within the condition classes. These characteristic time periods will, at equilibrium, be similar to the 'passage time' and 'mean lengths of stay within a class' for Markov models.

Starvation. We note that 'starvation' can only apply to individuals in the lowest condition class, and that this should be thought of as an additional risk of dying for that class only. While the model does permit the possibility that an animal initially in condition class i will eventually starve, it can only do so after a minimum of t = i time periods. The effects of class dependent mortalities from other factors, such as predation can be incorporated into the direct class mortality parameters and these do not, of course, operate with a time delay as does starvation (Figure 1).

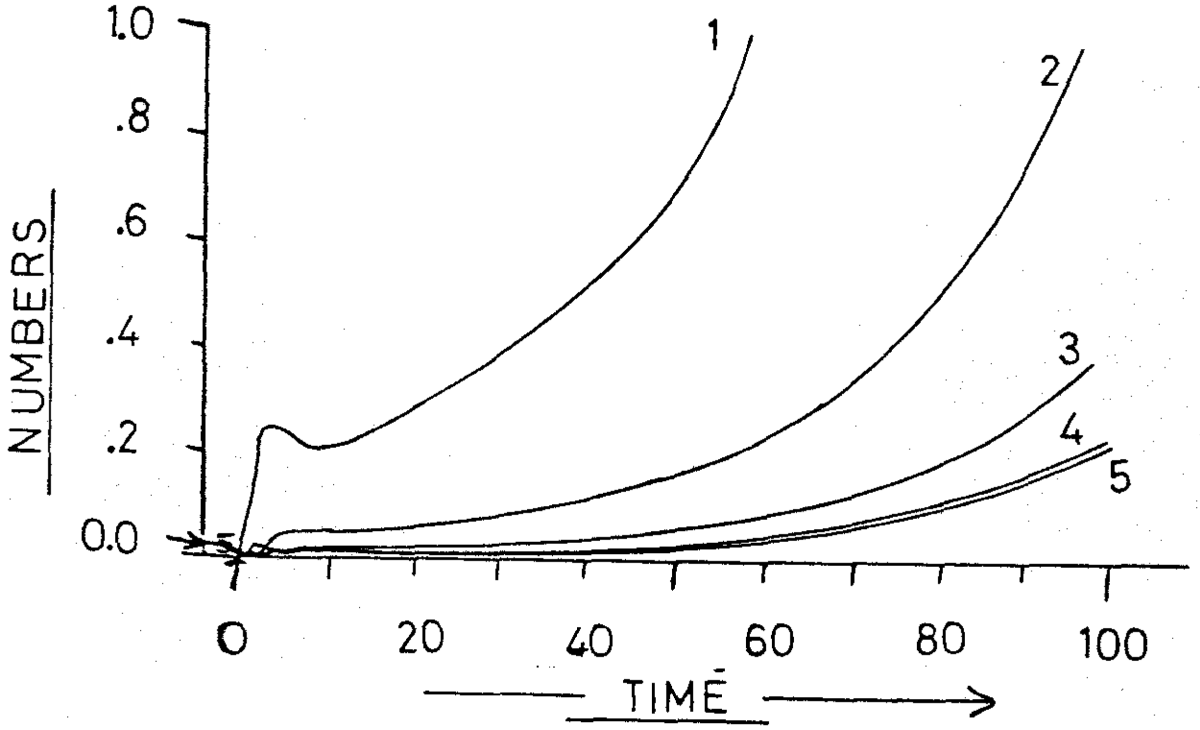
3.3 Unconstrained population growth

The use of the model for this simplest case is illustrated in Figure 1 by the output of a simulation program LOMNOC.BAS using hypothetical data for the transition matrix and starting, arbitrarily, with 50 individuals in the highest condition class. After an initial period of instability (about 10 time periods) the numbers of animals in each condition class rise, exponentially, at rates determined by the NET gains and losses as summarised in the transition matrix. Plotted logarithmically, the slopes of these lines would show the intrinsic rates of increase for the classes. Dominant eigenvalue and eigenvector would (presumably) also give the intrinsic rate of increase and the ratios of numbers per class at the stable composition, as they do for Leslie matrices.

Figure 1. Unconstrained population growth.

The figure show output from the simulation program LOMNOC.BAS, plotting numbers of individuals against time. The curves numbered 1-5 correspond to numbers in each of the five weight classes.

The two arrows at the origin indicate the number of class 5 individuals used to 'start' the simulation at time zero. Note the initial instability, followed by gradual increases in all weight classes.



3.4 Constrained population growth

3.4.1 Constrained population growth: general

The model, as described above and illustrated in Fig. 1, is extremely limited (as are simple Leslie Matrix models) in that there is no stable equilibrium: the population either increases or decreases exponentially, except for a (unique) unstable equilibrium.

In classical population dynamics, stability is usually enforced by a <u>constraint</u> on the population size that limits <u>net</u> growth with respect to some hypothetical density (carrying capacity, K), eg. equations 2.2 → 2.7. This is little more than a mathematical fudge factor to ensure that $N_{t+i} \rightarrow K$. The precise form in which N_{t+i} approaches K will depend on the function used (here $\frac{K-N}{K}$ assumes the rate is linearly proportional to the difference in densities N_t and K). Other formulations can be used, but there is little detailed theoretical justification for them, nor is there, for most species, an easily definable concept for K, far less an adequate definition by which it might be measured in the field.

Similar restraints may be incorporated in matrix models of population growth: readers interested in the details of these procedures should consult, eg. Usher (1966, 1976) and Beddington (1975). In the present model of population condition and growth a formulation that is rather realistic for many populations may be suggested.

Assume that there is a maximum amount of food available in the environment of the population, K_F, capable of supporting a biomass, K, of animals. There will, due to random effects, be some flux of individuals from one condition class to another, as suggested by our previous matrix formulation. However, if, at any time t, the total biomass of the population, K_P, exceeds that which can be supported by the environment, K, then some individuals will be unable to maintain their condition, due to lack of food. Assuming that the time period, t, is sufficiently short for only slight loss of condition we could envisage these animals passing from there current class C_i to class C_{i-1}, this loss of weight being directly due to competition for the limiting food resource; the restriction that those individuals who lose condition and start from class C_1 will starve to death similarly applies. We could envisage this competition taking either of two extreme forms, commonly termed 'scramble' and 'contest' competition in the literature, and defined below in the context of these models:

'Scramble' competition assumes that individuals get, or fail to get, 'enough' of the limited resource entirely at random, ie. independent of any phenotypic characteristics of those individuals. In the context of our 'condition' model scramble competition implies that mortality induced by lack of the limiting resource would be independent of the condition class, C_i, of the individual. While such a situation is rather against the tenets on which the model is founded, it is perhaps possible to envisage environmental restraints that might impose such an effect (unpredictable and heterogeneous distribution of food within the environment). More importantly, it forms an interesting special case, as it amounts to a formulation of the condition hypothesis in the absence of social dominance hierarchies which can then be used as a null hypothesis to investigate the effects of such hierarchies. For this special case we could describe the difference between restrained and non-restrained populations by the formula:

$$C_i = K/P \,.\, C_i + (1 - K/P).\, C_{i+1}$$

Where C_i = condition class, $i = 1, n$

K = carrying capacity biomass

P = projected biomass in absence of competition

and with the mathematical assumption that $C_{n+1} = 0$, or the obvious restriction that the second term does not apply when $i = n$.

FIGURE 2a: Flow chart of computer algorithm for SCRAMBLE competition.

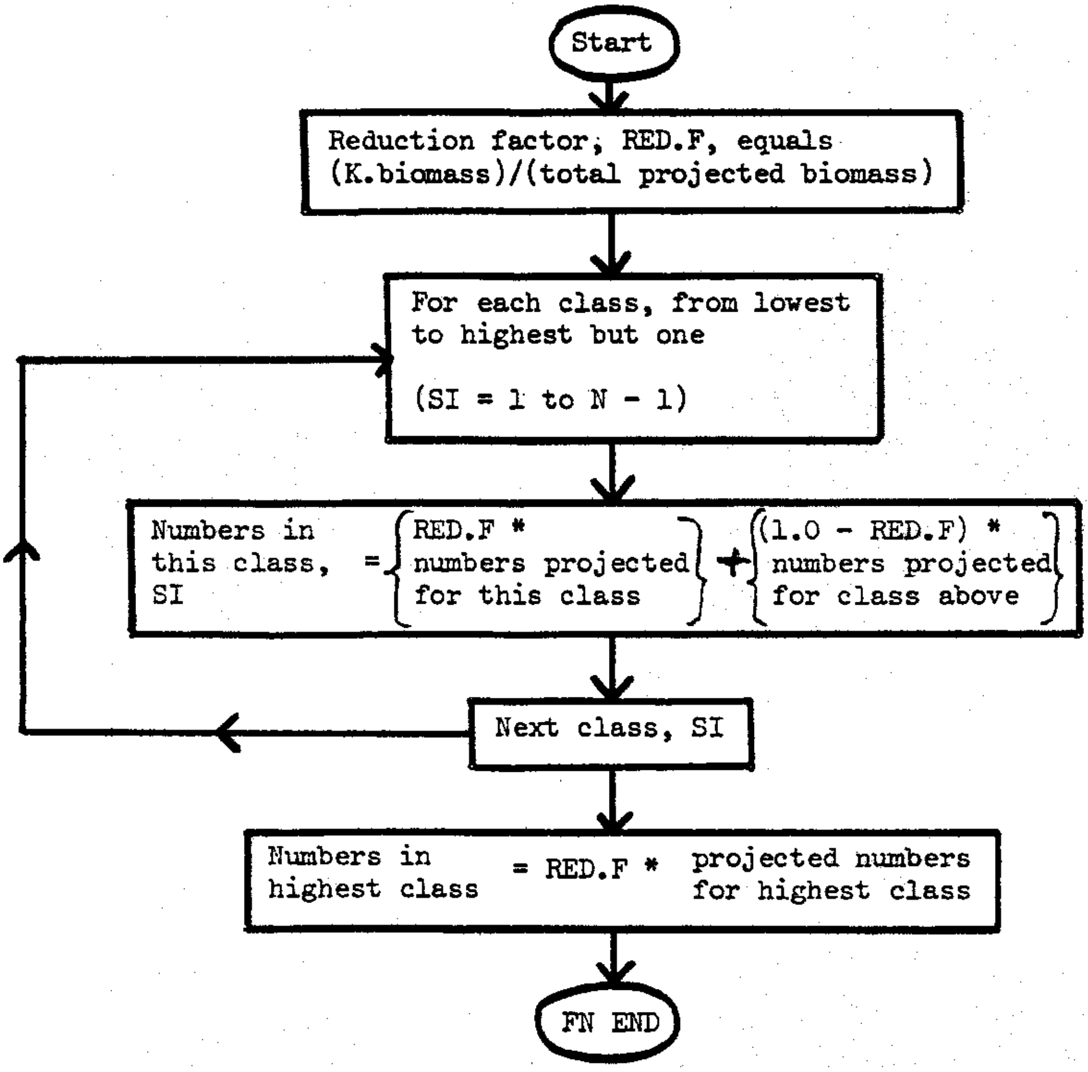
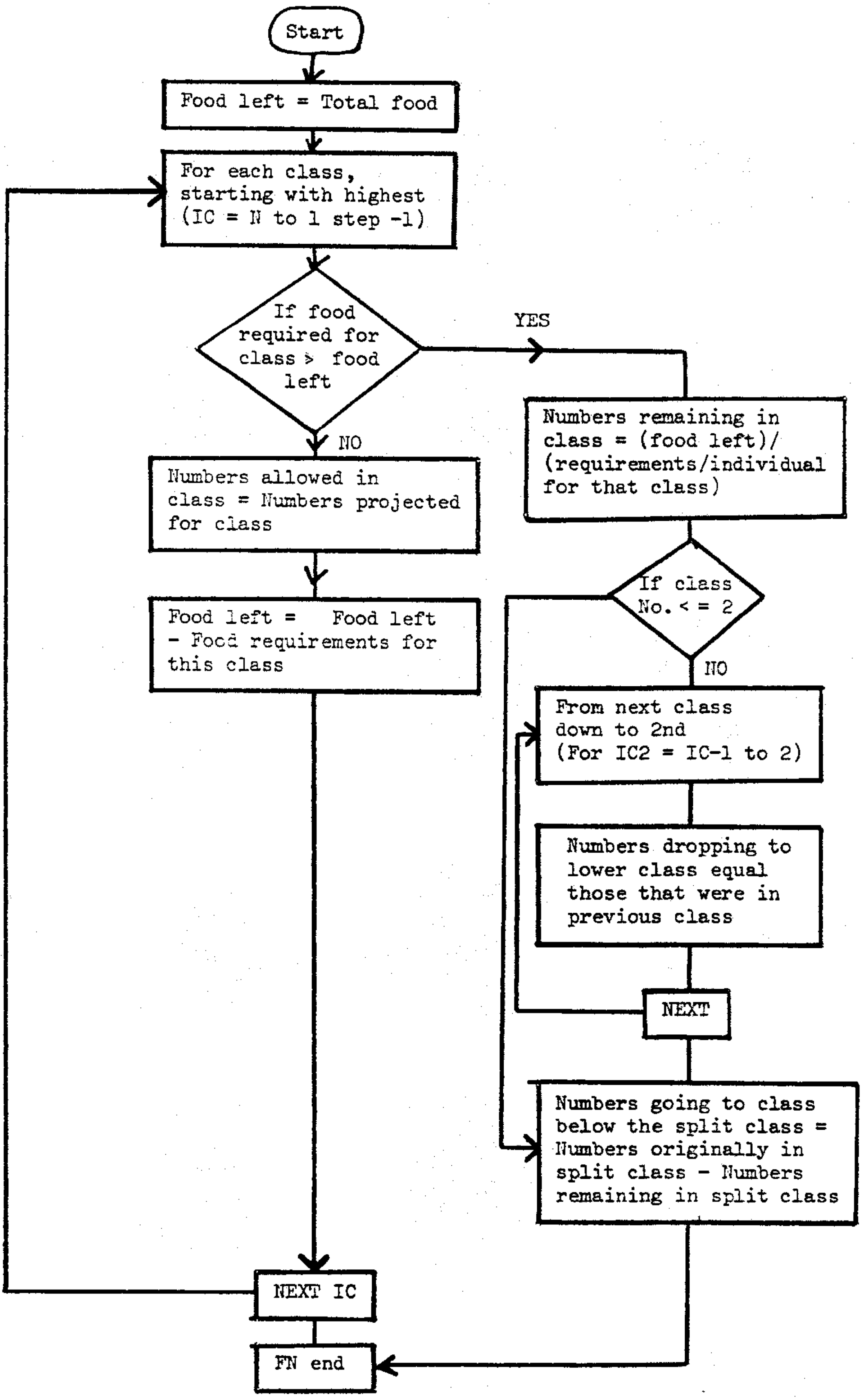


Figure 2b: Flow chart of the computer algorithm for CONTEST competition.

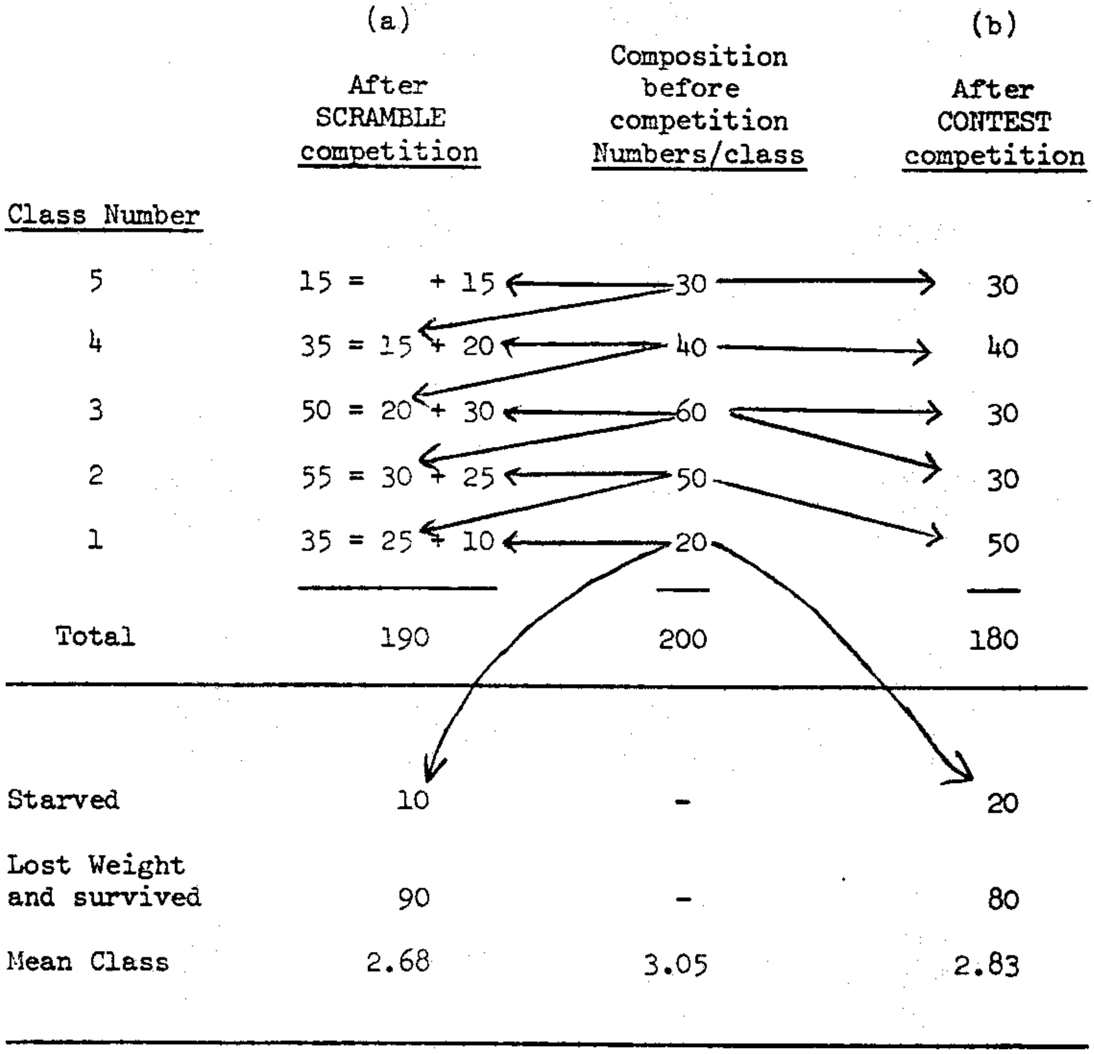


This formula enforces the dichotomous assumption that each individual can (at random for scramble competition) either (i) maintain the condition it would have achieved in an unrestrained population or (ii) survive for the current time period by using some of its own body's food resources to supplement its diet, thereby losing weight/condition during the period. Note that this puts a restriction on the time period selected in relation to the class interval. A worked example of such changes is shown in Table 2a.

In summary I should emphasise that the effects of 'Scramble' competition as here defined are not random with regards to mortality. The effects of 'Scramble' competition give random allocation of resources to individuals, with consequent random probability of weight loss to those individuals but, because the model assumes only lowest condition animals will die as a result of weight loss, the mortality effect of Scramble competition is not random among the classes.

'Contest' competition. The same dichotomous options apply, namely (i) survive and maintain weight or (ii) survive by using body resources and thereby lose weight, but the probabilities of the two events are now considered to vary depending on the condition/weight of each individual. 'Contest' competition implies that the partitioning of resources depends on the outcome of contests between individuals (sometimes physical combat, but often special displays or an established dominance hierarchy/peck order, after which the 'winner' gets as much as it wants and the loser gets the remainder, or nothing). In species for which there is either a well defined dominance hierarchy or in which display/combat success is closely related to physical condition we will not go far wrong if we assume individuals high in the hierarchy always win in contests with those much lower in the hierarchy. Accordingly given an amount K of limited resource, it will be partitioned according to the rule: 'those highest in the hierarchy get all they want, until there is none left; below this critical level, the remaining individuals get nothing, so ALL those below that level must use body resources to survive and will hence lose weight'.

TABLE 2: Assume an initial population of 200 individuals divided among 5 weight classes as shown in the central column. For arithmetic simplicity assume that any individual from any class requires 1.0 units of food to survive and maintain weight. Given a total of 100 units of available food, the changes due to SCRAMBLE and CONTEST competition will occur as shown in columns (a) and (b) respectively.



Class Number	(a) After SCRAMBLE competition	Composition before competition Numbers/class	(b) After CONTEST competition
5	15 = + 15	30	30
4	35 = 15 + 20	40	40
3	50 = 20 + 30	60	30
2	55 = 30 + 25	50	30
1	35 = 25 + 10	20	50
Total	190	200	180
Starved	10	-	20
Lost Weight and survived	90	-	80
Mean Class	2.68	3.05	2.83

<u>Summary</u>

With SCRAMBLE competition only 10 individuals starve, but 90 loose weight so that the mean class level drops more, to 2.68.

With CONTEST competition 20 individuals starve, but only 80 loose weight and the resulting mean class level drops less, to 2.83.

We may express this in Flow diagram form, as shown in Figure 2b.

The possibility that some individuals low in the hierarchy are more efficient feeders than some individuals higher in the hierarchy is accounted for in the model by the probabilities of weight gaining and weight loss, see Table 1c.

3.4.2 A model of a population limited by competition for resources

Having defined our concepts of SCRAMBLE and CONTEST competition for a limited food resource of amount K, we can now envisage an iterative simulation model of the form shown in Figure 3.

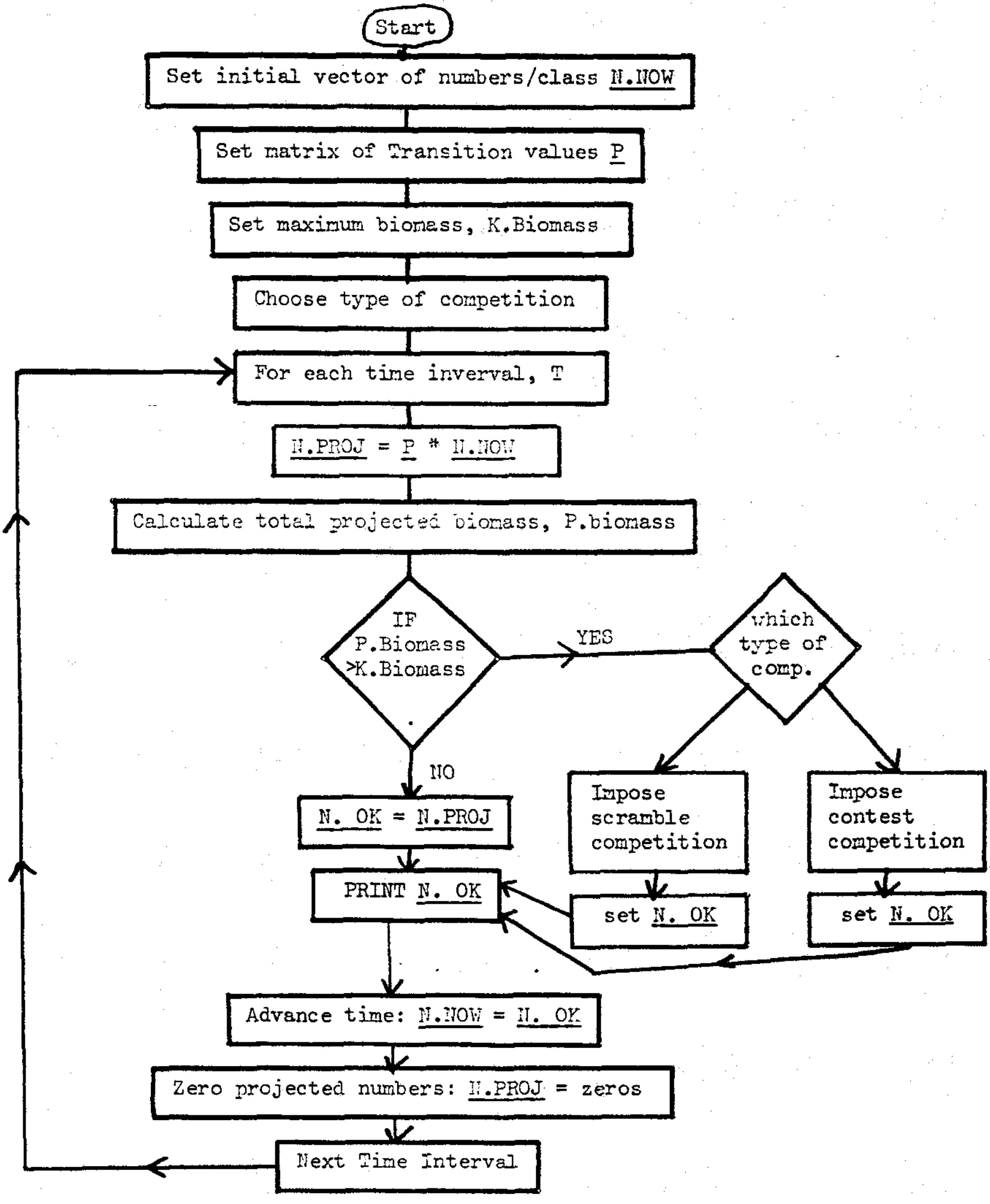
Effectively the transition matrix $\underline{P}$ (of fecundity, growth, maintenance or loss terms) determines what happens unless the projected biomass exceeds that which the food supply can support. If it does exceed this threshold, K, then the vector of projected numbers in each class $\underline{\text{N.PROJ}}$ must be reduced according to the rules of the selected mode of competition (EITHER contest OR scramble).

For the simple flow diagram of Figure 3 to be strictly applicable, we are making the following assumptions:

i. offspring reared into particular classes do not compete for 'parental' food until they reach that class. This is equivalent to saying either that they use a qualitatively different food resource OR that food is effectively super-abundant during the rearing period OR that their parents supply it for them, etc.

ii. the time of food shortage must be short, so that the amount of weight lost between one class and the next would be sufficient to provide the animals' maintenance energy for the whole of that time interval

Figure 3: Flow chart showing the main portions and sub-routines of the 'competition' model of population dynamics LOMUO3.BAS. Note the position of the * in the flow chart, which indicates where K (K.biomass) is varied each time united in the subsequent program LOMSR2.BAS, described below.

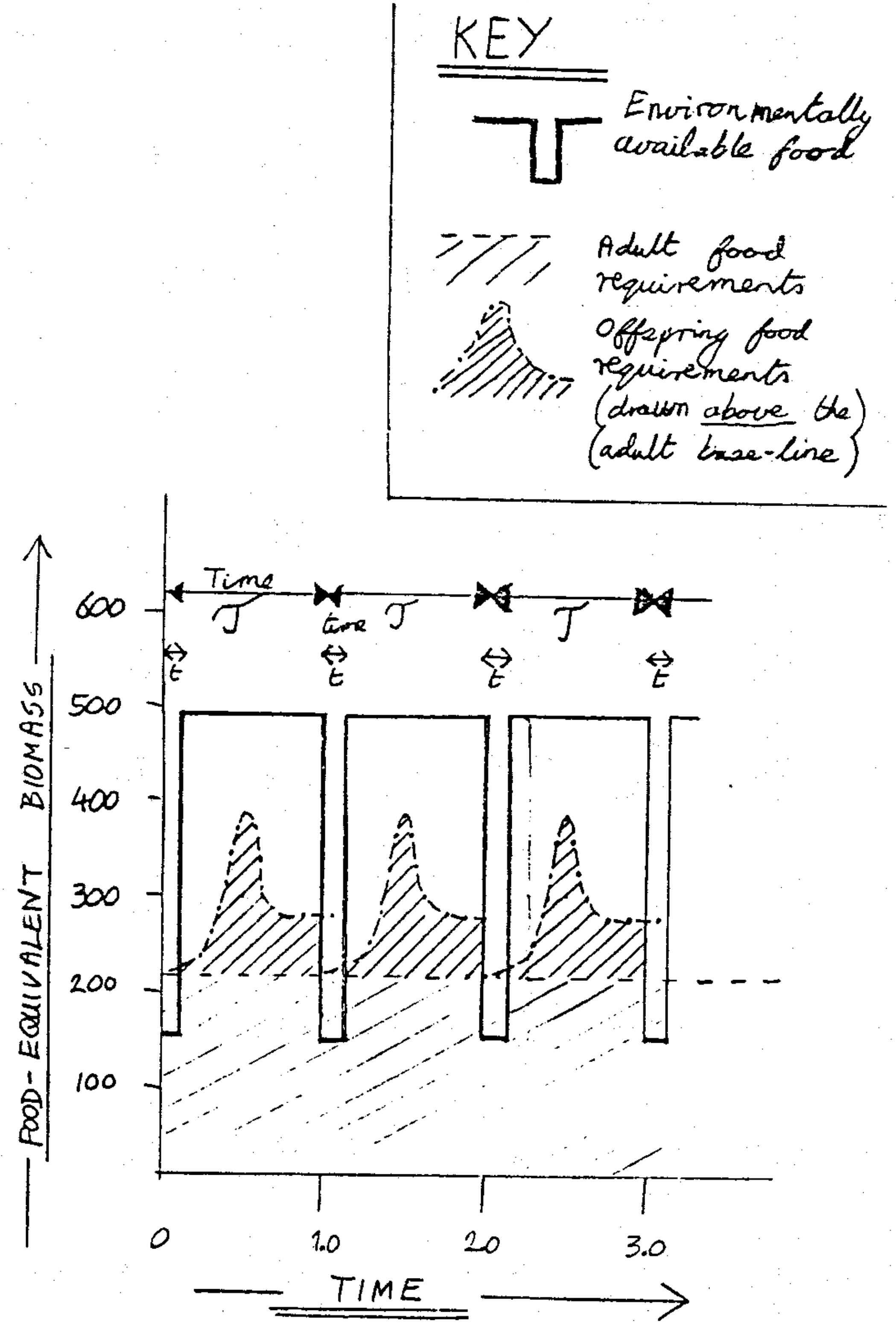


*K.Biomass = K.biomass - (RND (x))

FIGURE 4

The figure illustrates patterns of food demand and supply that would meet the assumptions of the model program LOMU03.BAS.

Note that the exact form of the Available Food line is not important, only that it should exceed Demand for the period shown. This point is considered in more detail subsequently; see, eg. Figure 14.



iii. energy requirements are proportional to body mass for all individuals (this assumption could be relaxed, see below).

These assumptions would be met by idealised circumstances as shown in Figure 4, which effectively permits us to apply the restraint of a short interval t to a longer interval T, as there are no restraints whatever operating outside t.

The results of such simulations are shown in Figures 5a and 5b, for Scramble and Contest competition respectively. The values in the transition matrix, $\underline{P}$, are identical to those used in the example of Figure 1. It can be clearly seen from the figures that, after initial periods of instability the population numbers rise (identically to Fig. 1 for the first 47 time steps), until the 'threshold' is reached. Thereafter the population composition fluctuates briefly, and eventually reaches a stable composition. We note particularly: first that these stable compositions are different for Scramble and Contest competition; secondly that the time taken to reach the stable level after the threshold has been reached is shorter for Scramble, compared to Contest competition. Third, the populations reach the same stable weight distributions if initial numbers are below or above the limit imposed by K.

In summary the effects of Scramble competition produce an equilibrium population comprised of **more** less-fit individuals whereas, conversely, Contest competition produces an equilibrium population of **fewer** more-fit individuals.

3.4.3 Age structures

I emphasise here that the stable levels illustrated in Figure 5 refer to numbers of individuals in each 'condition' class and not to the age structure. However, as indicated in the introduction, the model provides a diverse series of pathways for getting from one weight class to another. For example 'lucky' individuals might, with low probability, go

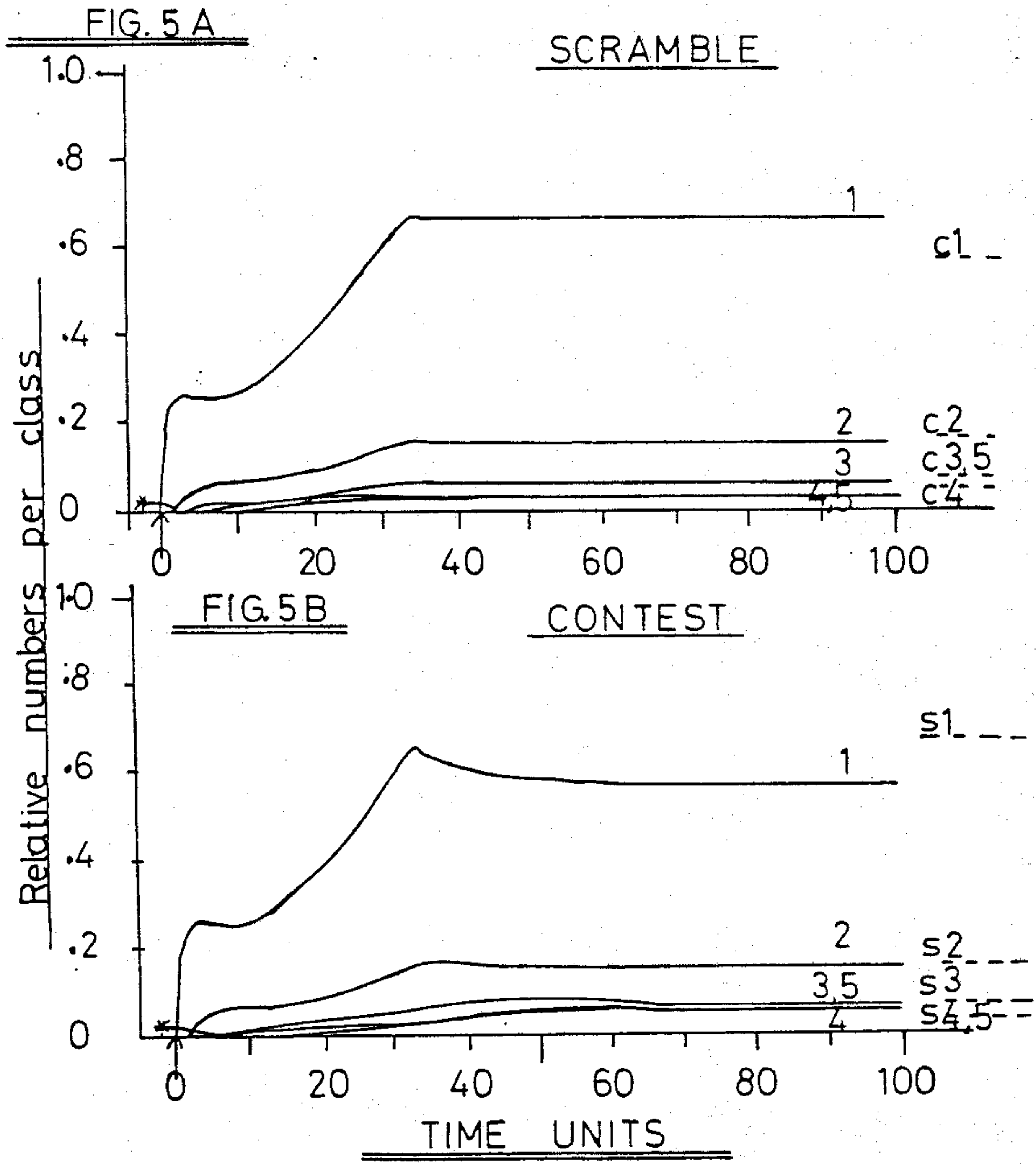
Figure 5. The figure shows changes in numbers of individuals per weight class (classes numbered 1-5) against time periods of the simulation model. The populations are limited by the same amount of 'available food equivalent', and both start from an initial composition of 50 Class 5 individuals at time t=0, (see * at figure origins).

In Fig. 5A the population is constrained by SCRAMBLE competition.

In Fig. 5B the population is constrained by CONTEST competition.

Note that both types of competition lead to stable levels of all classes (class numbers given above right hand end of the solid lines representing the classes in each figure).

The levels reached by the classes under the OTHER type of competition are shown by the numbered dotted lines in each figure to emphasise that the classes reach different stable levels for the two types of competition.



from class 1 to class 5 in just four time periods; other individuals might take longer, spending some periods only maintaining weight, or losing and then regaining weight; yet others might gain weight initially then lose it all and starve; and so on. At equilibrium, for either type of competition, we can hence envisage a variety (= to the number of classes, C) of distributions of ages within weight classes, which could be illustrated as a set of C histograms (% frequency per age class) for <u>each</u> weight class C. Conversely we would envisage a set of histograms giving the % of individuals <u>of a specific age</u> (a = 1, ...A) in the different weight classes.

At this stage I will just comment that a stable age structure will (or at least is very likely to) exist. Methods for finding such stable levels have been developed for Markov models, and for variations of Leslie Matrix models (eg. Usher, Beddington). It is possible that similar algebraic approximation techniques could be developed for the present models. If this proved too complex, the age distribution(s) could nevertheless presumably be discovered by extensive use of random numbers within constraints given by the outputs of the present model.

3.5 Seasonal variation

The model described in the previous section has assumed that the environment of the population is homogeneous in both space and time. Spatial heterogeneity is fairly complex, and is considered briefly below, but temporal variations can, at least for variations in the important parameter K, be quite readily introduced.

In the following example we will confine temporal variation to the actual amount of food, K, available in given time periods, T. While it would be quite possible to consider K_t as a function of environmental variables (eg. $K_t = f(e_{1t}, e_{2t} \ldots e_{Et})$) we will for purposes of illustration, here assume that the available food in a given time period, K_t, varies at random within the interval K_{max} to K_{min}.

Figures 6A and 6B. The figures show the effects of environmental variation on the equilibrium levels of the Weight Classes.

Environmental variation is expressed as percent variation of K.biomass below its maximal level: a maximum value for this variation is set as V% (plotted on the abscissa) and varied randomly for each time unit of the simulation according to a uniform random distribution. The numbers of individuals per class, averaged over 50 time periods at equilibrium, are plotted logarithmically as the ordinate. Figure 6A is for SCRAMBLE competition and Figure 6B for CONTEST competition.

The mean class level, the standard deviation and the standard error are shown for each class, together with their sums, representing the effects of the total population.

Note that class levels drop most for SCRAMBLE competition and have more similar variability.

FIG. 6A

SCRAMBLE

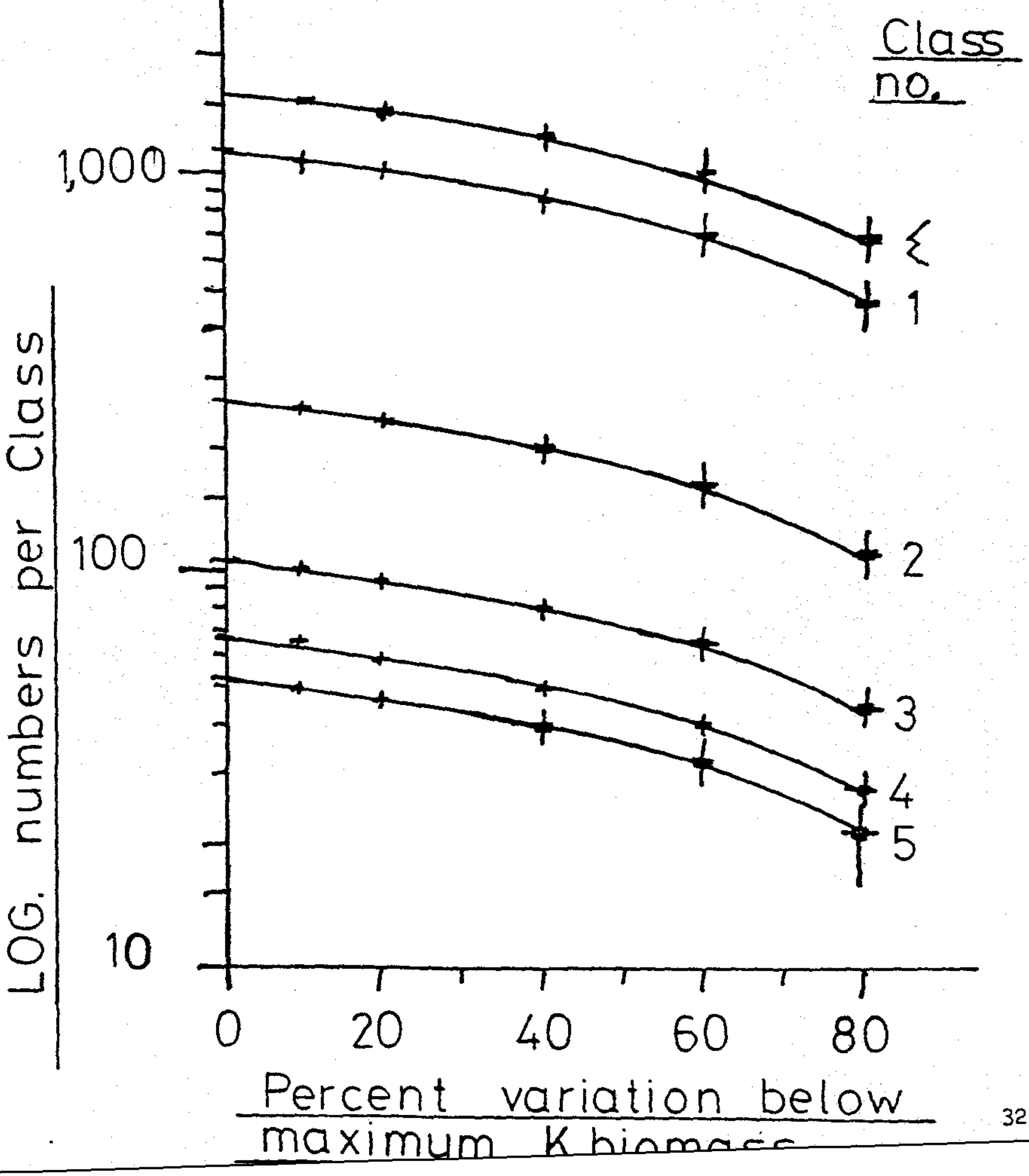
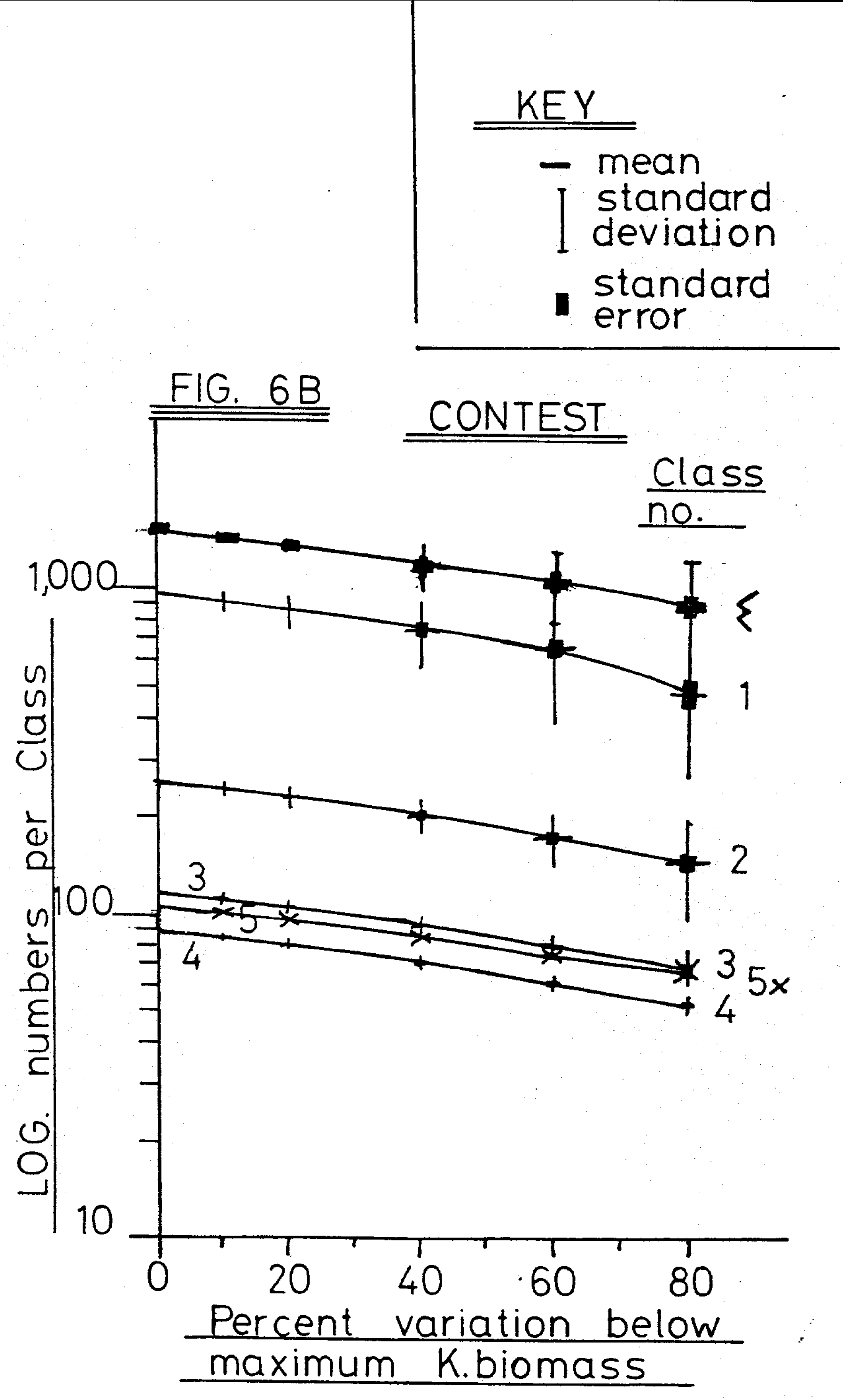


FIG. 6B


KEY
mean
standard deviation
standard error
CONTEST
Class no.
LOG. numbers per Class
1,000
100
10
Σ
1
2
3
5
4
3
5×
4
0
20
40
60
80
Percent variation below maximum K.biomass

This option has been introduced into a second simulation program LOMSR2.BAS, identical to the first except that it allows the value of K_{min} to be set on input, and that it varies K (K.biomass) during the time loop, by the use of a random number generator (see * in Fig. 3). A routine to average the levels of each class over a chosen period of time is also included to facilitate comparisons of different outputs from the model.

The equilibrium results of such simulations, again using the same transition matrix P as for Figs. 1 and 4, are shown in Figs. 6a and 6b for Scramble and Contest competition respectively. These figures plot, on a logarithmic scale, the average number of individuals in each weight class 1-5 (and their total) for increasing amounts of variation of K below its maximal level. For SCRAMBLE competition, Fig. 6a, it can be clearly seen that the total, and all classes, drop considerably as the environmental instability increases. Note particularly that the Standard Deviation bars fall well below their stable levels for a uniform environment (indicating that for a very high proportion of the time the population is below this level. N.B. the distribution will be skew, so precise interpretation is difficult) and, indeed, that for extreme variations (>40%) the class levels would remain permanently below the stable levels they achieve for a uniform environment (twice the standard deviation bars is still below the level for uniform conditions). For CONTEST competition Fig. 6b, the situation is markedly different. The total level, and all class levels drop relatively less, and the upper standard deviation limits are much closer to the appropriate levels for uniform conditions, showing that the population is depressed less continuously than is the case with SCRAMBLE competition, for the same amount of environmental instability. This point is further emphasised in Figures 7a and b (for SCRAMBLE and CONTEST competition respectively) which plot, for each class, the coefficients of variation of class numbers against % environmental instability. The coefficients of variation rise appreciably, and fairly consistently for all classes for SCRAMBLE competition. With CONTEST competition the rise is much less for the higher weight classes (4 and 5), about the same for class 3 and very much more for classes 1, 2 and the total. This reflects the fact that

Figure 7. The figures show for SCRAMBLE and CONTEST competition respectively the effects of environmental variation (as defined in the text and legend to Figure 6) on the variation of numbers of individuals per class. This class variation per time period is expressed as the Coefficient of Variation (Standard deviation bars of Fig. 6 divided by mean level from Fig. 6) and plotted linearly as the ordinate on Figures 7.

FIG. 7

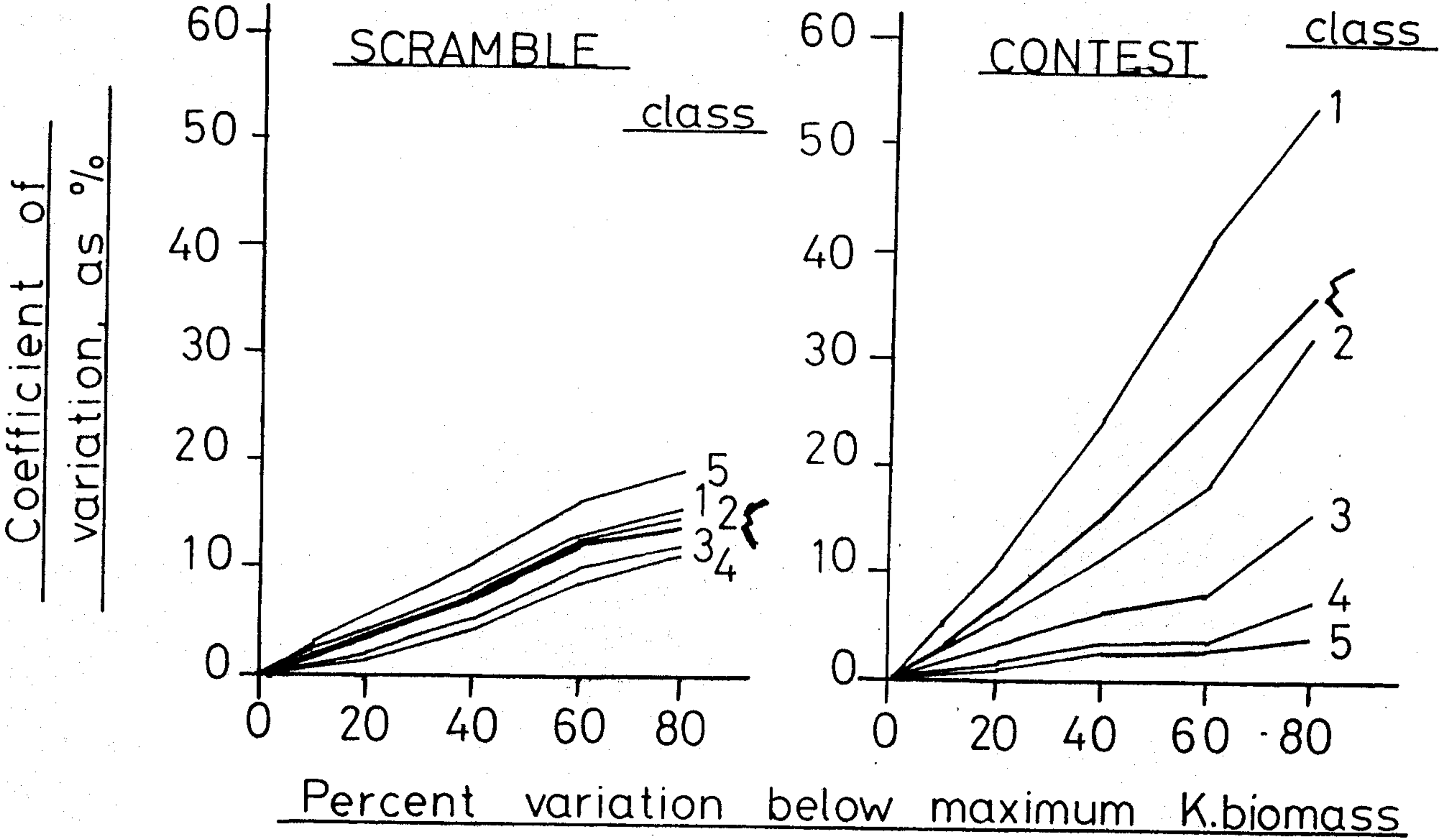
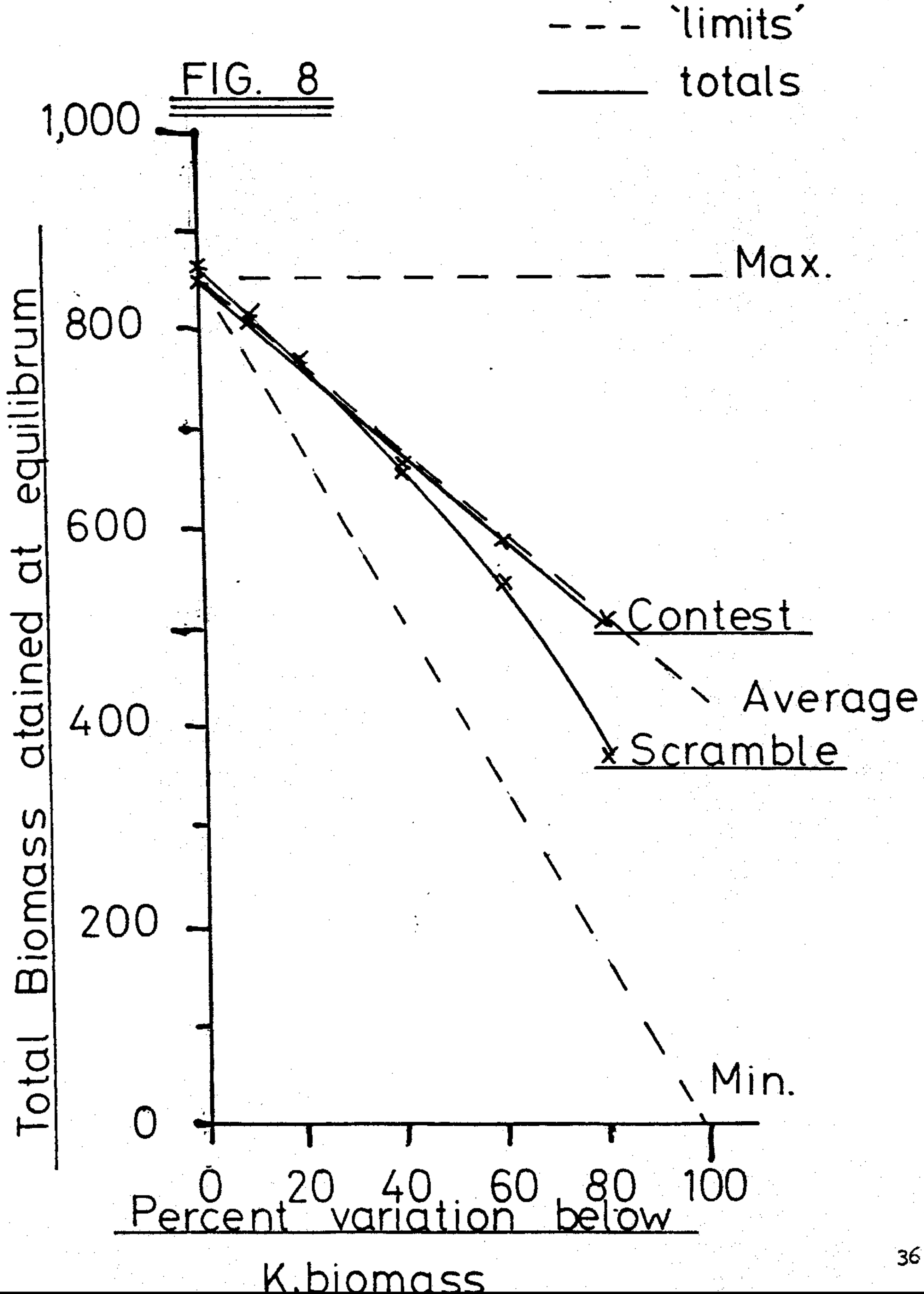


Figure 8. Average biomass attained by populations at equilibrium for SCRAMBLE and CONTEST competition for varying amounts of seasonal variation of food, K.biomass, expressed as percent below maximum available.

The figure shows Maximum, Average and Minimum 'food supported' levels and levels attained by the simulated populations.

SEE TEXT for details. Data set 1, 'Old Matrix' values.

FIG. 8



SCRAMBLE competition affects all classes and (for the values of growth, death and fecundity used in this P matrix) causes the breeding numbers to be depressed to a level so that they cannot so readily take the population back to a high level following a 'crash'. CONTEST competition on the other hand maintains higher numbers of 'breeders' (see Fig. 6), and the population is able to respond much more rapidly to increases in food which may follow a sharp decline. This is illustrated in Figure 8, which plots the average total biomass attained by populations constrained by SCRAMBLE and CONTEST competition against % environmental instability in K.biomass, indicating the maximum level of K and the average level of K for that variation. We note that CONTEST populations are consistently close to the average availability, whereas SCRAMBLE populations drop well below this level for variations above 50% in K.

If we examine Fig. 8 in detail we see that, for SCRAMBLE competition at low variations (<20%), the attained biomass actually exceeds the average available. This is possible because an excess of individuals are produced during the period of super-abundant food (see Fig. 4) and, even at equilibrium, some of these survive by losing weight (ie. by utilising food 'stored' during the unlimited growth period). Such an argument also applies to CONTEST competition, but if we look at the average CONTEST line in Figure 8 we see that it never exceeds the available average. This is not inevitable however, rather it is an artifact of the values of this example data-set in the P matrix and the rules of CONTEST competition. The reasons for this restriction can be seen by examining Table 3 which shows, for both CONTEST and SCRAMBLE competition, the steps involved in the calculation of changes in numbers per class for a single time interval at the equilibrium conditions of Fig. 8. For CONTEST competition classes 2-5 reach equilibrium immediately after fecundity and mortality in the 'plentiful' food period ($\underline{P} \times \underline{N}_{t+1}*$): only class 1 has an excess of numbers under CONTEST rules, and as by definition these must maintain weight or starve, there can be no excess biomass surviving. Conversely, for SCRAMBLE competition all classes are in excess of their equilibrium numbers at time $t+1*$ (after the 'plentiful' period and before SCRAMBLE competition mortalities); consequently a small excess biomass, from classes 2 to 5, survive by utilising resources accumulated in the 'plentiful' period, and this mass is in excess of K.

TABLE 3

The table shows the stages of calculation at equilibrium numbers for CONTEST and SCRAMBLE competition.

The transition matrix, <u>P</u>, is multiplied by the vector of equilibrium numbers, N_t, to give the projected numbers <u>after</u> 'growth' and fecundity but before competition-induced mortality, column $N_{t+1}*$.

The next two columns show the biomass calculations to determine the excess of projected biomass, P.biomass, over environmentally supportable biomass, K.biomass.

The final column, $N_{t+1}^{\ddagger}$, shows the final conditions after one stage of the whole process, which represents a return to the equilibrium conditions (shown initially in column N_t).

Note that with CONTEST competition classes 2-5 reach equilibrium numbers at column $N_{t+1}*$, but class 1 only at column $N_{t+1}^{\ddagger}$, whereas no class regains equilibrium numbers until $N_{t+1}^{\ddagger}$ for SCRAMBLE competition.

<u>CONTEST</u>

CLASS	TRANSITION MATRIX from class 1	2	3	4	5	N_t	$N_{t+1}*$	$N_{t+1}*$	c=1 Mass, c=5 t+1*	Hence class 1 survivors are		givin $N_{t+1}^{\ddagger}$
1.	.50	.14	0	4.50	5.50	965.0	1517.6	7588.0	11262.0	(8500-3675)/5 = $\frac{4825}{5}$	=	965.
2.	.10	.58	.10	0	0	275.9	257.9	1418.5	3675.0			257.
3.	.0	.13	.64	.10	0	118.1	116.1	708.6	2256.6			116.
4.	0	0	.16	..67	.10	90.0	90.0	603.3	1548.0			90.
5.	0	0	0	.18	.85	108.0	106.0	918.0	918.0			106.

<u>SCRAMBLE</u>

CLASS	TRANSITION MATRIX from class 1	2	3	4	5	N_t	$N_{t+1}*$	$N_{t+1}*$	Survive and maintain weight x 0.932	Survive by reducing weight x 0.068	$N_{t+1}^{\ddagger}$
1.	.50	.14	0	4.5	5.5	1132.2	1194.3		1113.1	19.0	1132.
2.	.10	.58	.10	0	0	267.7	279.2		260.2	7.5	267.
3.	0	.13	.64	.10	0	106.9	109.8		102.3	4.5	106.
4.	0	0	.16	.67	.10	66.0	66.7		62.2	3.9	66.
5.	0	0	0	.18	.85	53.4	57.3		53.4	-	53.

<u>Weights vector</u>

CLASS	WEIGHT
1.	5.0
2.	5.5
3.	6.0
4.	7.0
5.	8.5

$N_{t+1}*$ = numbers after fecundity and 'random mortality but BEFORE competition induced changes

$N_{t+1}^{\ddagger}$ = equilibrium numbers AFTER competiti induced changes.

TABLE 4: The effects on the equilibrium conditions for SCRAMBLE and CONTEST competition of altering the structure of the P matrix by introducing a fecundity value ($\neq 0$) on row 2, and mending the value of element 1,5 so that class 5 parents still produce the same biomass of offspring. The effects of this change in structure on the equilibrium conditions are small for SCRAMBLE competition but very marked for CONTEST competition.

The Model's data

Class weights	Data set 1 'old' P Matrix					Data set 2 'new' P matrix				
5.0	.50	.14	0	4.5	5.5	.50	.14	0	4.5	4.0
5.5	.10	.58	.10	0	0	.10	.58	.10	0	1.0
6.0	0	.13	.64	.10	0	0	.13	.64	.10	0
7.0	0	0	.16	.67	.10	0	0	.16	.67	.10
8.5	0	0	0	.18	.85	0	0	0	.18	.85

Equilibria for UNIFORM model

SCRAMBLE

	Data set 1 'old' P equilibrium	Data set 2 'new' P equilibrium
1.	1132	1035
2.	268	348
3.	107	130
4.	66	74
5.	53	52
Σ mass	8690	8823

CONTEST

	Data set 1 'old' P equilibrium	Data set 2 'new' P equilibrium
1.	965	30
2.	258	596
3.	118	273
4.	90	208
5.	108	249
Σ mass	8500	8648

We may confirm that the apparent restriction of the equilibrium mass for CONTEST competition shown in Fig. 8, is due to the structure of the P matrix by altering its values. Changing the transition probabilities would clearly alter drastically the equilibrium values, but we would expect, and can confirm from (unillustrated) simulations, that changes to the fecundity values (to, eg: 0, 0, 0, 5, 6.5; or 0, 0, 0, 4, 6) do not greatly alter the equilibrium numbers for SCRAMBLE or at all for CONTEST competition and that the equilibrium mass for CONTEST is still restricted to K. This is true for a wide range of fecundity values (so long as overall production exceeds overall mortality).

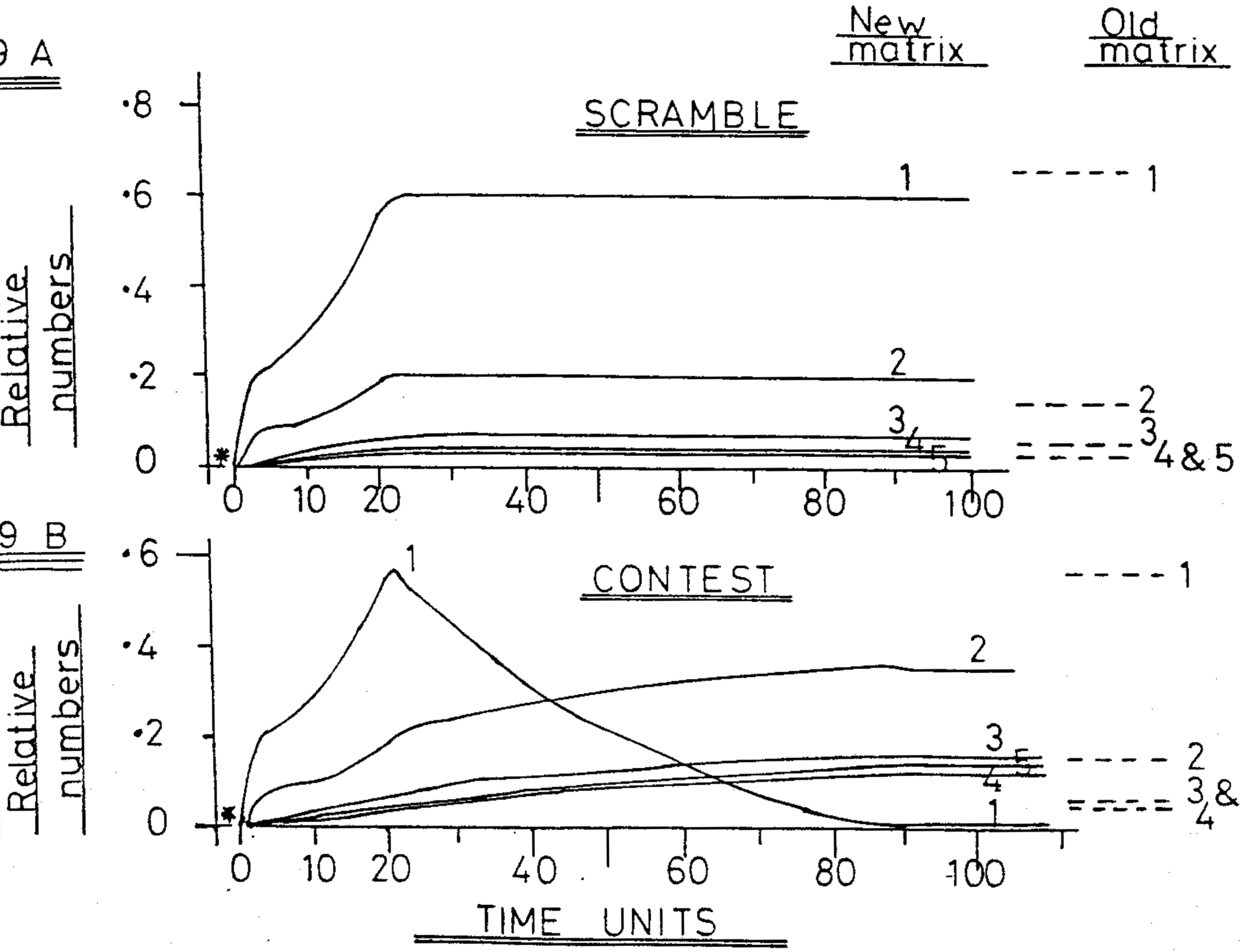
However, if we change the P matrix's form so that individuals can be 'reared' into class II, as shown in Table 4 (note that the total mass of offspring reared by class 5 individuals is the same for the 'old' and 'new' P matrices of Table 4) we remove the restriction on the equilibrium mass for CONTEST competition and, moreover, change the basic dynamics and equilibrium conditions for both SCRAMBLE and CONTEST competition, as shown in Figure 9.

Figure 9a illustrates the situation for SCRAMBLE competition using the new P values. As in Fig. 5a the class numbers rise smoothly to a stable level, and remain there. Class 1 is the commonest, as before, but there are <u>fewer</u> class 1 individuals, more individuals in classes 2 to 4 than previously (see Table 4a) and a greater overall biomass than formerly. Figure 9b and Table 4b show the new equilibrium for CONTEST competition, and the change is much more dramatic than for SCRAMBLE. Contrasting Fig. 9b with Fig. 5b we see the uniform initial rise, as formerly, with class 1 individuals rapidly becoming the commonest. However, when competition actually takes effect (about time unit 25) class 1 drops very rapidly in numbers, becoming rarer than class 2 by time T = 50, rarer than classes 3, 4 and 5 by time T = 70 and falling to a stable, extremely rare level by time T = 90. Hence altering the fecundity values to permit 'rearing' of individuals into class 2 (see Table 4) has slightly altered the relative frequencies of the classes for SCRAMBLE competition, while retaining their rank order, but has drastically altered the population structure for CONTEST competition by changing class 1 from the commonest

Figure 9. The figures plots numbers of individuals per weight-class (classes 1-5) against time in the simulation model, using the values from the 'New' transition matrix and for both SCRAMBLE (Fig. 9A) and CONTEST (Fig. 9B) competition.

The levels for each class are shown by the solid lines in the figures, each line being identified by a class number above it at the right of the figure (Heading New matrix). The dotted lines appearing to the right of the figure show the levels reached by those classes (numbers and lines appear under the heading 'Old matrix') using the 'Old' transition matrix for comparison. (See Figure 5 for an identical plot as to how these 'Old' levels were reached).

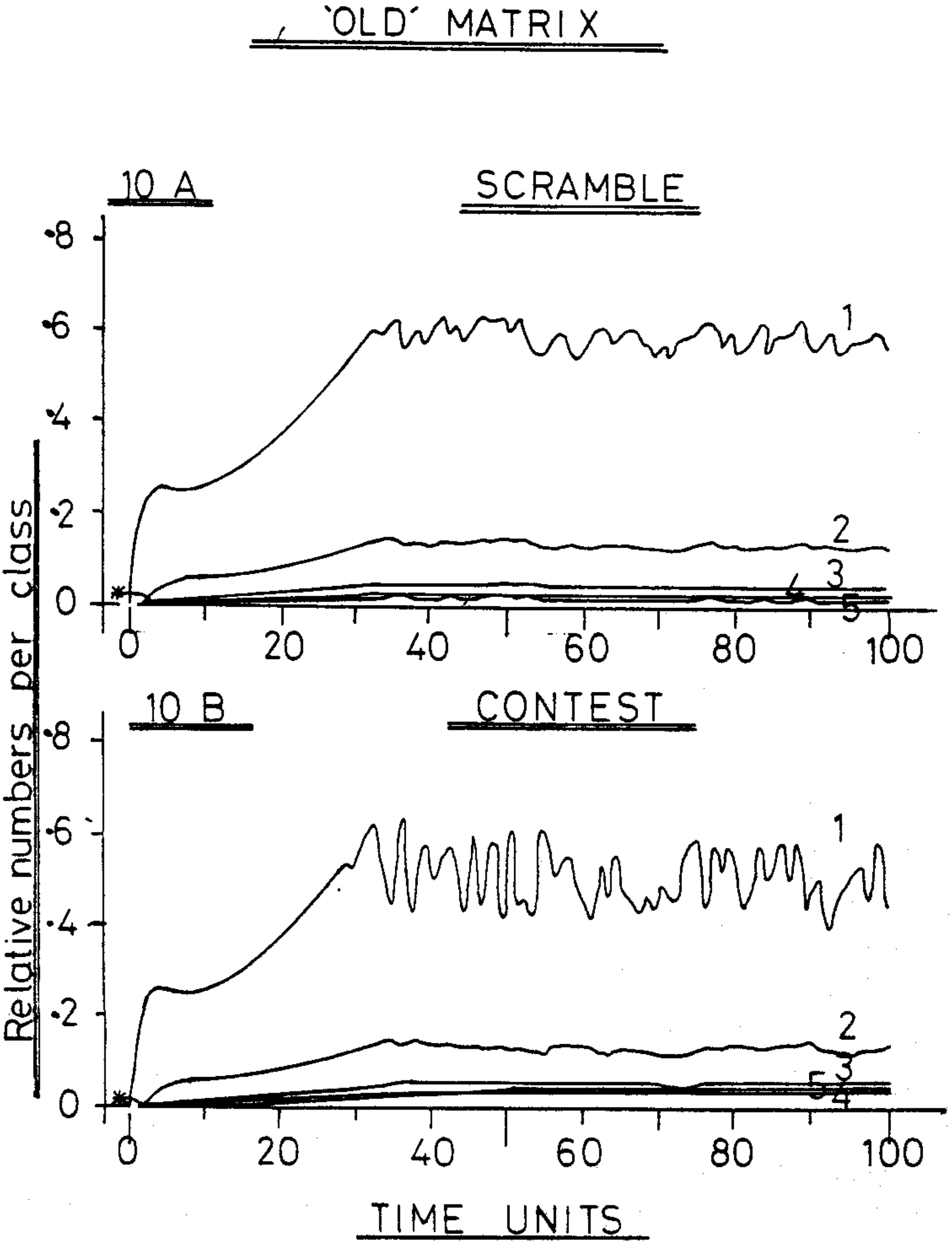
Note that while the general levels and relative order of the classes for SCRAMBLE competition (Fig. 9A) are quite similar for both transition Matrices the outcomes under the different transition matrices are dramatically different for CONTEST competition. In particular, under CONTEST competition, class one changes from being by far the commonest to by far the rarest, with consequent dramatic changes in the absolute levels of classes 2-5.



Figures 10. These figures (10a and 10b) are directly comparable with Figures 5a and 5b. They show variations on numbers of individuals per weight class for each class 1-5 against time in the simulation model, starting from 50 class 5 individuals. However, Figures 10 are results from the program LOMSR2.BAS, which varies the 'carrying capacity', K, at random for each time unit of the simulation.

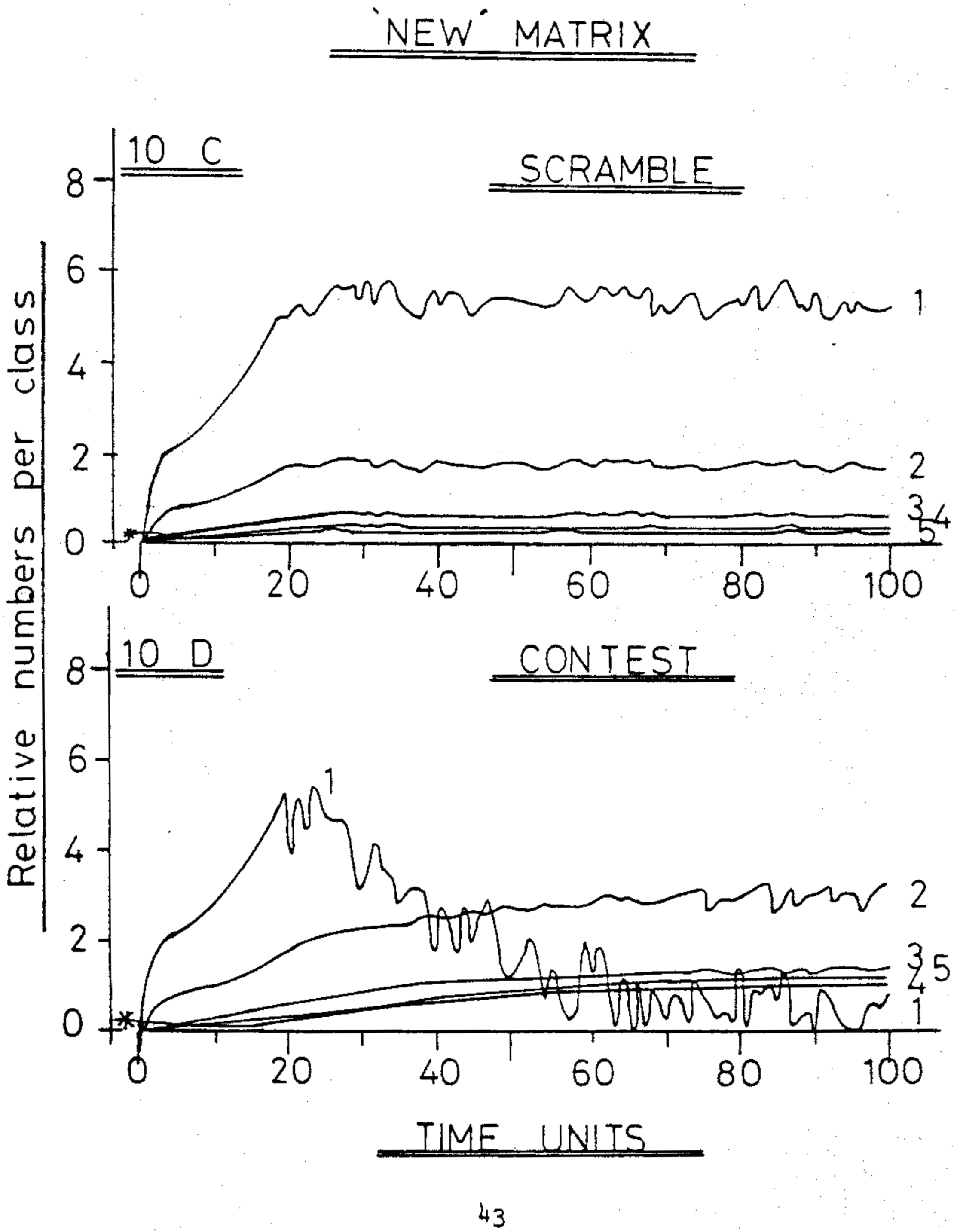
For these two figures K was varied randomly by a maximum of 20% below its maximal value (value used throughout for Figures 5, see text for details).

Note that the classes reach similar levels under both circumstances (compare 5a with 10a, 5b with 10b) but that the fluctuations of class 1 are more extreme with CONTEST competition.



Figures 10. These figures (10c and 10d) are included for direct comparison with Figures 10a and 10b respectively. All four figures are produced by the model program LOMSR2.BAS with 20% variation of K.

Note that, as illustrated in Figures 9, the use of the 'New' transition matrix, allowing animals to be 'born' into the second Weight-class dramatically alters the equilibrium structure of the population for CONTEST competition, but only has slight effect with SCRAMBLE competition.



to the rarest. We emphasise that the change in the P matrix is largely one of structure not values as the new fecundity terms for class 5 breeders result in the same biomass of offspring being reared per capita (see Table 4). Reference to the last line to Table 4b confirms that the equilibrium biomass for CONTEST competition (=8648) now exceeds the limiting value of K (=8500) whereas with the previous P matrix it was exactly equal to K.

We may now return to our model which accounts for variations in K (LOMSR2.BAS) and see the effects of the new P matrix values. With SCRAMBLE competition and 20% variation the basic situation is much the same (compare Fig. 10a and Fig. 10c) for both P matrices, but with CONTEST there are marked differences (Figs. 10b and 10d). Essentially classes 1 and 2 respond dramatically to variations in K under CONTEST competition and it is this which permits CONTEST populations to stay permanently close to the actual limits of available food. This effect is summarised in Fig. 11 (which may be compared with Fig. 8 to show the different effects of the two P matrices).

Examining Figure 11 in detail we see that, at zero variation in K, SCRAMBLE populations attain higher sustained biomass than CONTEST populations, as before (see Fig. 8) but that the CONTEST population is now also above the K 'limit' (see also Table 4). As variation in K increases, SCRAMBLE populations do less well (relative to the average of environmentally supportable biomass): at 20% variation they are only as successful as CONTEST populations; at 50% variation they fall below the 'average sustainable level'; at 90% variation they are slightly closer to the minimum sustainable level than to the average sustainable level. CONTEST populations however maintain a fairly constant excess of attained biomass over average supportable biomass until there is 60% variation in K below its maximum: subsequently the average biomass attained by CONTEST populations drops only slowly, reaching the average supportable level at c. 85% variation of K and not being far below the average at 90% variation of K. This is again due to the higher proportion of breeders present in CONTEST populations producing a more plentiful crop of offspring, as is shown by comparing Figure 12a with Figure 12b. The

Figure 11. Average biomass attained by populations at equilibrium for SCRAMBLE and CONTEST competition for varying amounts of seasonal variation of food, K.biomass, expressed as percent below maximum available.

See Figure 8 for comparison and legend, and see text for details.

Data set 2, 'New Matrix' values.

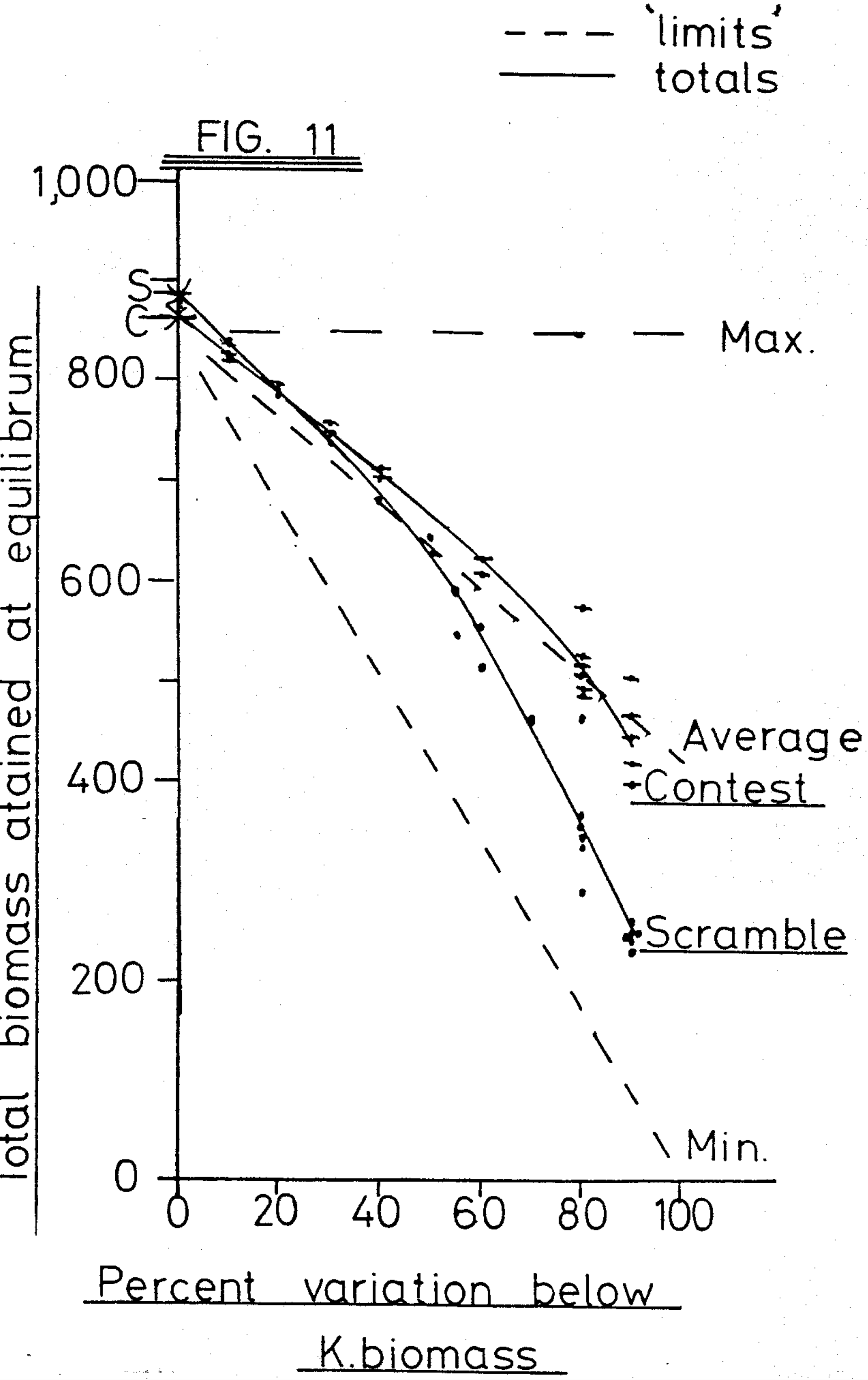


Figure 12. Effects of environmental variation of available food, K.biomass, on equilibrium numbers of individuals per weight class. See Figures 6 for comparison of these results, obtained with Data-set 2 ('New Matrix' values), with the previous results from the 'Old Matrix' values (Data-set 1).

Note particularly the dramatic effect of the new data values on the outcome for CONTEST competition. Weight class 1 changes from being the rarest, on average, with zero variation of K. biomass to the commonest, on average, with 90% variation, while its variation per interval becomes extreme (see off-set error bars).

FIG. 12

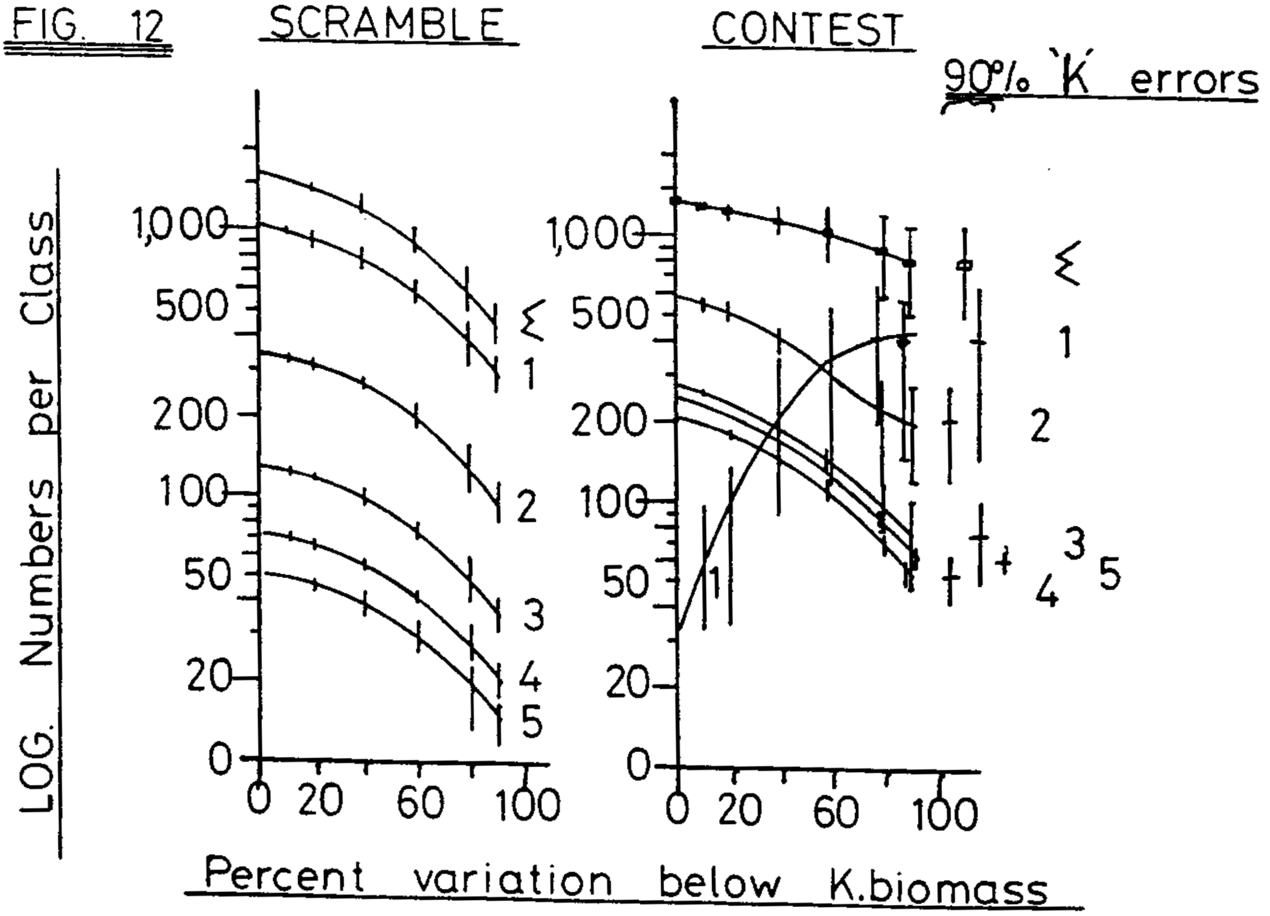
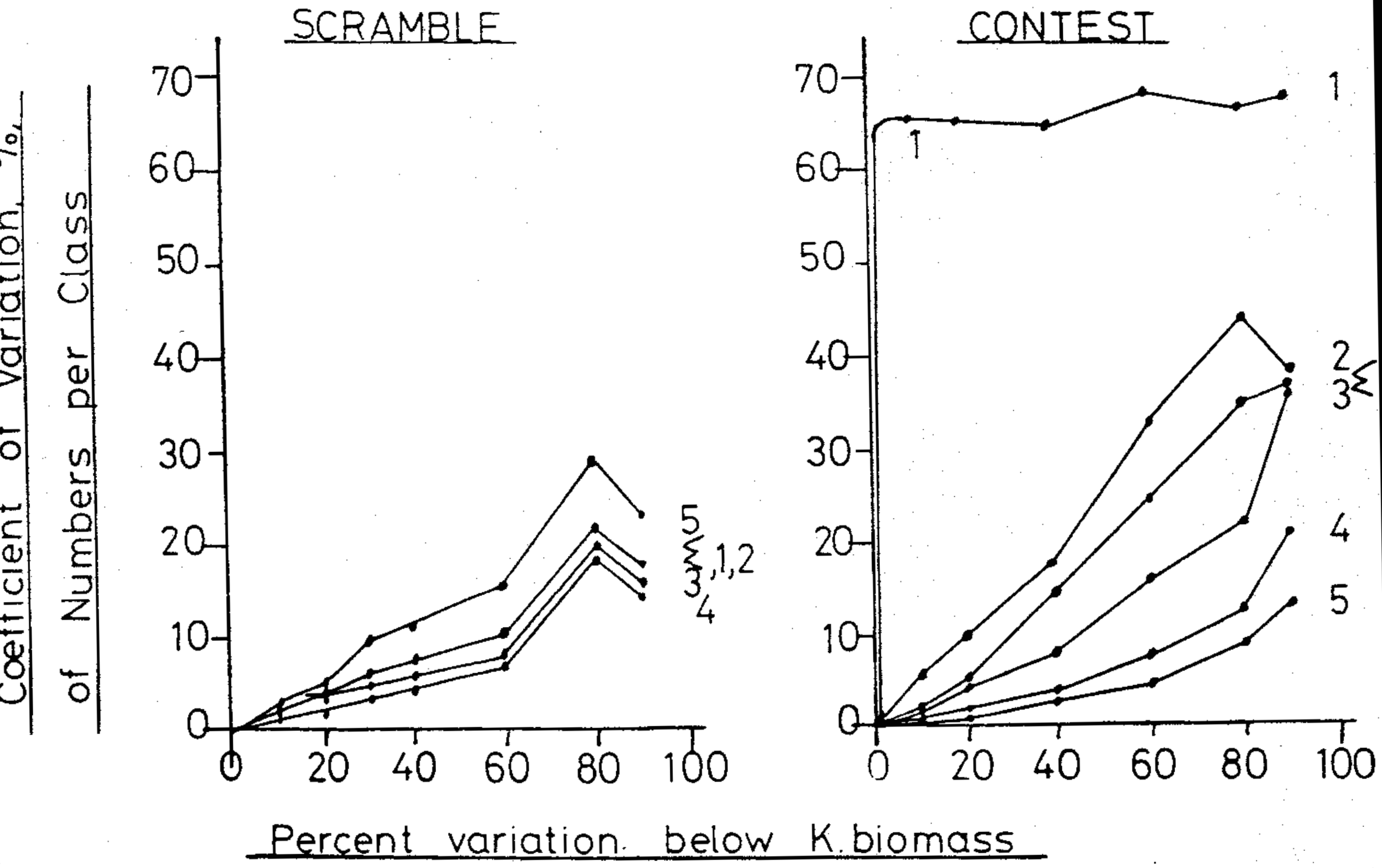


Figure 13. Effect of environmental variation of K.biomass on the variability of numbers of individuals per Weight class, expressed as the coefficient of variation of Numbers per Class for different levels (%), of variation of K.biomass.

See text for details and Figure 7 for comparison.

These results are obtained with data-set 2, note effect on class 1 with CONTEST competition is dramatic.

FIG. 13



average number of class 1 individuals for CONTEST populations rises dramatically as variation of K increases, and examination of Fig. 10d confirms that they reach high numbers very irregularly as food happens to be available. This variation is illustrated in Figure 13, which plots coefficients of variation, for each class, against % variation in K. It is interesting to note that for CONTEST competition the coefficients of variation tend to rise consistently as environmental variation rises, but for SCRAMBLE competition the coefficients of variation peak at around 80% and then drop. This may be interpreted as the level of variation the SCRAMBLE population is least able to cope with: at lower levels of variation (50%) SCRAMBLE populations achieve fairly stable composition close to the average level of food availability; at high level of environmental variation (c. 90%) they become constrained to a composition closer to the minimal supportable level (see Figs. 11 and 12).

4 FEASIBLE ELABORATIONS TO THE MODEL

4.1 More complex seasonality

In the previous section we introduced the possibility of variations of K with each time unit, but retained the restrictions that (i) competition did not directly affect the numbers of offspring reared and (ii) that food was only limiting for a short period of each breeding cycle (see Fig. 4). By elaborating the model's structure it is quite possible to cope with more complex situations, as, for example, when food availability limits a female's ability to produce eggs (or offspring for viviparous animals) or when (winter) food supply is limited for a more protracted period (the limit set on our current model is that the single period of limited food must be sufficiently short for an individual to survive for that length of time solely by using food resources equivalent to the difference between one class and another).

Consider a time period T (such as a year) broken up into S seasons (months), as shown in Fig. 14. Food availability (mass/animal equivalent mass) is shown by the solid line, and varies seasonally, being, say K_s, for each season, on average. If we assume an initial population equivalent in size and composition to the equilibrium population at the onset of the reproductive period (R_0 in Fig. 14) and assess its food requirements so that (i) each individual grows and reproduces unconstrained by lack of food and (ii) no individual starves due to (winter) decrease in food we could construct a curve, shown dotted in Fig. 14, of 'idealised food demand'. We might expect a real population to behave as indicated by the chain-dotted curve in Fig. 14: during winter it is a little above the immediate limit of food availability (due to utilisation of stored resources); in spring it rises slowly above this level as food becomes more plentiful (we follow Perrins 1970 in assuming that, due to the required growth period of offspring and their energy demands, individuals are likely to be obliged to lay eggs before food availability reaches a peak); in summer it rises dramatically as

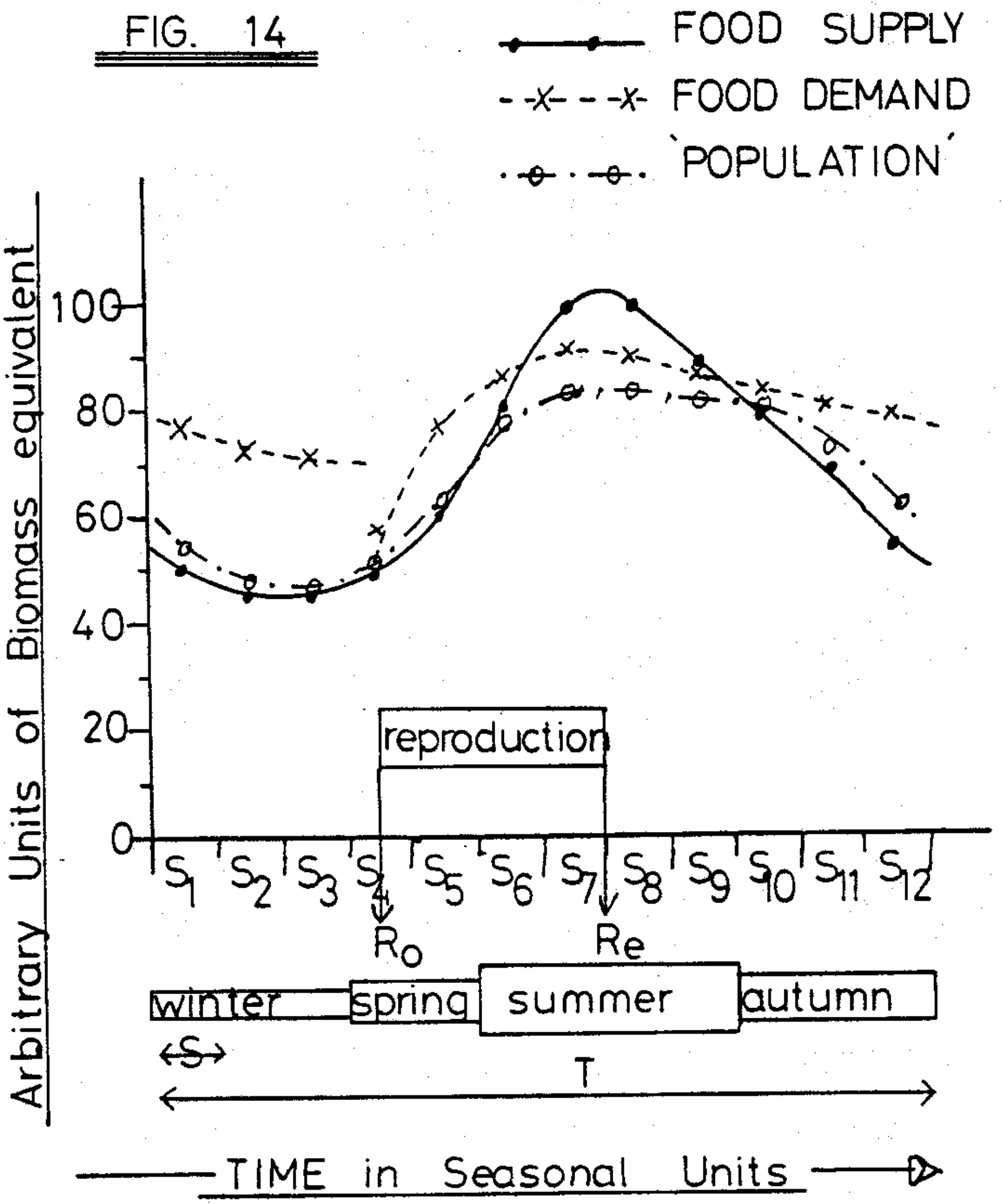
Figure 14. Hypothetical seasonal variation in the biomass of a population that could be supported by environmentally available food over one season.

'FOOD SUPPLY' - biomass that could be supported by the food at any instance IF there were that many individuals extant.

'FOOD DEMAND' - biomass equivalent of food that would be needed to support a population starting at the environmentally supportable level, at T=R (onset of breeding) IF there were to be no limitation on breeding or mortality due to lack of food resources.

'POPULATION' - likely course of actual population given the restraints of 'FOOD SUPPLY'.

FIG. 14



offspring are produced and use food to grow, but, due to the restraint mentioned above, is likely to remain below the available food and so may relax restrictions due to competition for a period; in autumn, food becomes less plentiful, and the restrictions of competition again take effect, causing the actual population level to drop.

We can envisage capturing this seasonal complexity by having a series of S transition matrices, $\underline{P}_{sij}$, that correspond to the transition probabilities for that season. In unrestrained conditions (relative to food supply) these matrices again represent the probabilities that, in a locally heterogeneous and unpredictable environment, a given individual will (a) find less food than normal, and lose weight (b) find enough food to maintain weight, (c) find enough food to gain appreciable weight or (d) die due to density independent causes. The total mass of such an unrestrained population would accordingly follow a track like that of the dotted curve of Fig. 14, assuming reproduction was limited to an appropriate period. If, for simplicity, we assume that births (= production and rearing of offspring to independence) takes place only once a year (or time period T) and always at a set time, (eg. T_{S5} in Fig. 14), then the model structure and simulation program would be quite straightforward. We would require, (i) S transition matrices $\underline{P}_{sij}$ (S = 12 for Fig. 14) of which only $\underline{P}_{5ij}$ would contain fecundity values, the others containing only transition probabilities and (ii) S values of K that would correspond to the solid curve in Fig. 14. Each matrix $\underline{P}_{sij}$ would be used in turn (S = 1-12; repeated for Y years): the population would be constrained by competition throughout but, as explained above, could (depending on the seasonal variation of K) be expected not to be <u>limited</u> by competition when food supply exceeded food demands. (We note, in passing, that Bacon (1981) has used such a series of matrices to model growth and competition of macrophytes in a river community).

For this special case (single broods at a specific season every year, offspring becoming independent within one time period S_s) the form of the model would be largely unaltered. We note that this simple model would permit us to investigate the effects of differing patterns of seasonal food availability in different years, and the effects of these on the numbers of breeding individuals (*ie.* investigating the results of different $\underline{K}(= K_s$, s = 1-12) vectors of food availability, either by using the same $\underline{K}$ every model year, but different $\underline{K}$ matrices for different runs, or by alternating one of a variety of $\underline{K}$ matrices ($\underline{K}_{vs}$) in different years for the same run of the model).

Further elaborations would be possible: multiple broods could be incorporated quite readily, so long as there was no period of parental care exceeding a time S (such a complication would require more complex structure of the $\underline{P}$ matrix and additional sub-routines), even allowing for a loss of condition causing time lags between production of one brood and the next.

4.2 Habitat heterogeneity

4.2.1 Background and theory

Studies of natural populations typically take place in a defined spatial area, often chosen largely for convenience rather than from more objective criteria. In consequence the results apply, in detail, to that area alone and can not be easily extrapolated to other sites. Contrasting results from different sites are difficult to compare because the habitats of each are often inadequately, or just differently, described. It is usual to find that the population processes are investigated in much more detail than the habitat composition or other environmental factors that underlie the causes of the population changes. There is consequently a need for population studies to be more closely linked to environmental aspects of the habitats on which much of the underlying population process are founded. Unfortunately, most models of population dynamics are for 'closed populations of random mixing individuals in homogeneous environments' and therefore explicitly ignore dispersal (migration and emigration) and effects of habitats. Dispersal from natal areas is poorly understood in ecology and it is often claimed that dispersal into sub-optimal areas cannot be an important mechanism of regulating numbers because it could not evolve by natural selection, as dispersal is disadvantageous for the dispersers (see discussion by MacArthur 1972). This argument is simplistic on two counts. First there is no reason to suppose the dispersing individuals 'intentionally' go into poorer habitat: they are presumably seeking for better conditions and, with no prior knowledge as to where such conditions exist, may go into, and perhaps never emerge from, less suitable areas. Dispersal, or emigration, clearly involves considerable risk that favourable conditions will not be found, but provides a potentially high reward (of favourable breeding) if they are found. Second, as pointed out by Lomnicki (1978, 1980) it depends on the assumption that all individuals are identical: following Lomnicki (loc. cit.) and the general theme of this paper we consider the situation for a population of animals in which resources are allocated unequally depending on condition or social dominance and emphasise that these differences need not, in anyway, be genetically determined. Consider a seasonally variable environment where winter food supply is typically able to support only half the summer numbers, or biomass, and allow some density independent mortality, say 10%. Starting with our rules for CONTEST competition, for simplicity, we consider the likely fates of animals in each third of the social hierarchy. Those in the top third have the standard 10% mortality risk, and a low risk that due to chance factors they will drop in the hierarchy, they are however, unlikely to drop a long way, below the critical half way mark, so their chances of neither starving nor losing weight are excellent. The situation for the middle third is more complex: those in the top half will generally stay there, and perhaps move up a bit due to random mortality of those above them (10% chance), and consequently those just below the mid-point may expect to move up slightly; those well below the mid-point will generally lose condition, although 'lucky' ones may do better, and others may lose condition appreciably. The situation is simplest for the lowest third: nearly all will lose condition seriously and most are likely to starve; the survival probability for this lower third can be thought of as being near zero. If we imagine this population to be in an isolated large patch of 'good' environment surrounded by a much wider area of 'poor' environment containing a few small paths of reasonable habitat, it is at once apparent that: (i) animals in the top third of the hierarchy should stay in the best patch, where they have high expectations of survival and good breeding (ii) animals in the middle third should also stay, as they are likely to survive and perhaps increase condition (iii) animals in the lower third are almost certain to die if they remain; even if the chance of maintaining weight in the surrounding area is about a quarter of that in the best area this is likely to be a much better survival prospect for those animals in the lower third. Accordingly we can presume that an animal very low in the social hierarchy at a time when food is scarce and competition ensues should move, in the 'hopes' of finding an area with less severe competition, as it is this competition which poses the greatest threat to such individuals ('one of the most important aspects of the environment to an individual is other individuals', Chitty 1966).

4.2.2 A simple model of heterogeneous habitats and dispersal

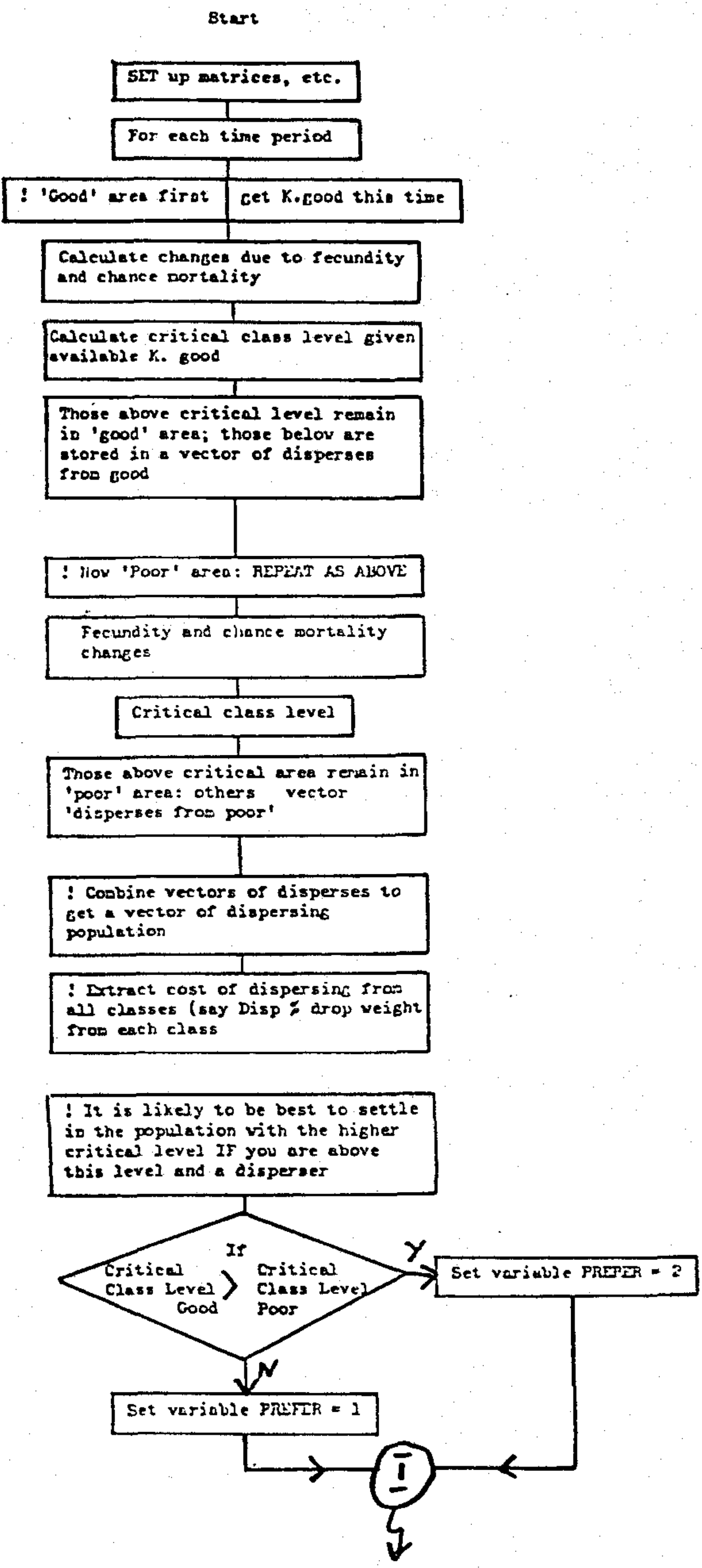
While it would be possible to develop a spatial version of the condition model to account in some detail for habitat heterogeneity and dispersal from a large patch of 'good' habitat to a larger surrounding patch of 'poor' area interspersed with some 'reasonable' regions this would be both rather complex and involve many more unknown parameter values. For illustrative purposes it is simpler to assume a mosaic of patches of 'good' and 'poor' habitat dispersed at random and to assume individuals have an average dispersal distance sufficient to take them from one patch, across the next, to a third. If we assume that dispersing individuals are readily able to assess *their* ability to gather food in the face of competition (the findings of J.R. Krebs and his colleagues lends credence to this simplifying assumption) then we may safely assume that dispersing individuals will (1) experience the conditions (*to them*) in both habitats and (2) will settle in the area most favourable to *them*. We emphasise that it is the conditions to the *disperser* which are important: while it is clear that a 'low dominance disperser' is likely to settle in the poor area, one can readily envisage conditions that might cause dispersal of 'high dominance' individuals *from* the poor area, and these might well be expected to have better prospects in the 'good' area if their condition puts them above the 'good threshold' level.

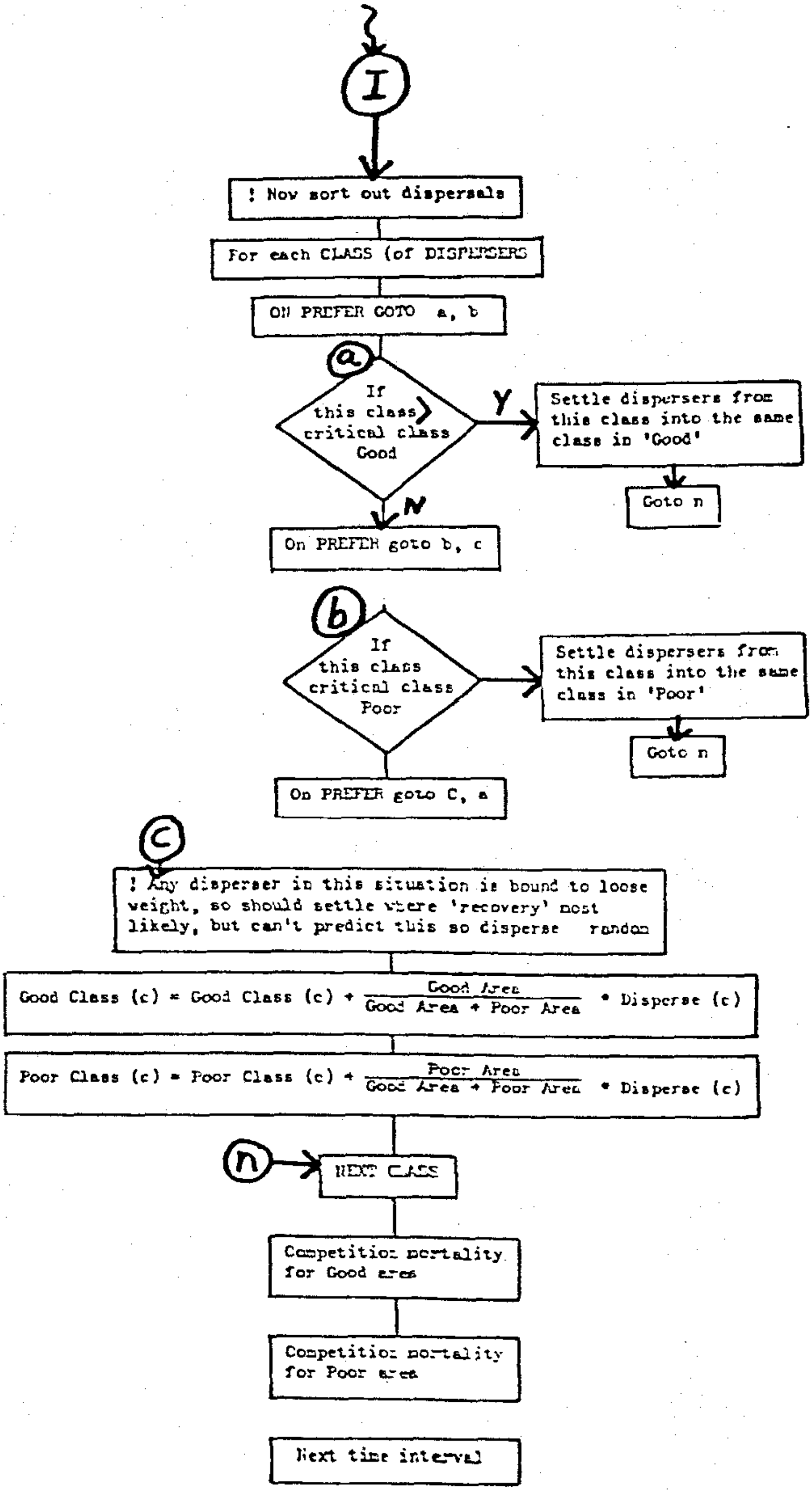
We must of course recognise that in some species dispersal will occur in relation to proximate factors rather than the ultimate factors that confer selective advantage to the dispersers ('Ultimate' and 'Proximate' are used sensu Lack, 1954). For example migrant birds disperse, or more precisely, migrate, in response to seasonal changes in day-length that signal, or 'give prior warning of' the onset of inclement conditions. Regular movements such as migration clearly require different treatment to that of short distance movements of individuals from non-migratory populations, as is envisaged in this discussion of dispersal.

The simplest dispersal situation to envisage would be to return to our seasonal model and assume two habitat types of equal food availabilities in 'summer' but diferent K maximum food in winter. K maximum would be the same in 'good' winters in both areas but the 'good' fluctuates little in bad years, say 20%, whereas the 'poor' area fluctuates a lot (say 80%). We could use the seasonal model to establish equilibrium conditions for both in the absence of dispersal, and then link the two simulations and look at (i) the linked equilibrium in 'good' habitat (ii) the linked equilibrium in 'bad' habitat (iii) the overall equilibrium conditions relative to the sum of the separated situations. The simulations could be linked along the lines shown in Fig. 15; the flowchart of Figure 15 is written principally for CONTEST competition, for which the process is more obvious. I do not suggest that the flowchart of Fig. 15 is an ideal way, far less the only way, of programming such a dispersal model, but consideration of this flowchart points to some of the possibilities and pitfalls. For example (see numbers on Fig. 15):-

i. We may assume that dispersal incurs some cost, and could account for this by assuming that a proportion of dispersers lose weight during dispersal (due to difficulties of finding food in unfamiliar and often poorer areas). This proportion could be varied in different runs of the program.

FIGURE 15: Flow chart showing how dispersal in relation to 'condition' could be simulated.




I
! Now sort out dispersals
For each CLASS (of DISPERSERS
ON PREFER GOTO a, b
a
If this class > critical class Good
Y
Settle dispersers from this class into the same class in 'Good'
Goto n
N
On PREFER goto b, c
b
If this class critical class Poor
Settle dispersers from this class into the same class in 'Poor'
Goto n
On PREFER goto C, a
c
! Any disperser in this situation is bound to loose weight, so should settle where 'recovery' most likely, but can't predict this so disperse random
Good Class (c) = Good Class (c) + Good Area / Good Area + Poor Area * Disperse (c)
Poor Class (c) = Poor Class (c) + Poor Area / Good Area + Poor Area * Disperse (c)
n
NEXT CLASS
Competition mortality for Good area
Competition mortality for Poor area
Next time interval

ii. It is possible, though unlikely, that high ranking individuals might be obliged to disperse from either area, but, depending on conditions in the other area they might be better off in the area from which they had come. It seems fair to assume that the best immediate prospects for an individual, if it is above the 'critical rank' in both areas would be to settle in the population with the lower critical rank, as it is then more likely to maintain its position above the critical level. It could presumably estimate the critical level, and the frequency distribution of the classes (which could indicate longer term suitability of the habitat?) through interactions with 'resident' individuals in the habitat.

iii. It seems clear that a disperser who is above the critical rank in any habitat should settle in one of these (preferably the 'best') but it is less clear what a disperser who is at about the critical rank in the lower of the two should do. It seems likely however first that it would do best to settle in that area whose critical rank is closest above it and second that there would be some uncertainty about both its own rank and its estimation of the levels of the populations' critical ranks. Accordingly the (integer) class inequalities > (see IIIs in Fig. 15) could well be replaced by >=.

iv. The immediate prospects for a disperser below the critical rank in both areas are poor (it is bound to lose weight and may starve) and, in theory, it should settle in the area likely to give it the better prospects of gaining weight in the future if it does survive. However, unless we endow our hypothetical animals with an inherent ability to assess habitat quality per se it is not clear that they could reliably assess this. The flow chart of Fig. 15 ignores this complexity, and settles them at random (in proportion to the areas of each habitat).

One could envisage programming a similar simulation of dispersal for SCRAMBLE competition, but (i) it would be much less clear how many individuals should disperse and from which classes, and (ii) how to determine where they settle, as SCRAMBLE competition implies that the presence of ANY extra individuals, (if biomass of animals exceeds available food), decreases weight maintenance prospects for ALL individuals of ALL classes, including themselves. This suggests that, in populations where SCRAMBLE competition applies, emigration cost-benefits would be extremely complex and uncertain. We might therefore expect that it would only be of a clear advantage to individuals in the lowest category (who are immediately doomed with high probability if they stay) and even then only if the cost of emigration were small (ie. if the prospects of losing weight during emigration and before finding a more suitable area are less than the prospects of losing weight in the present area).

4.2.3 Habitat differences affecting births and deaths

It would of course be straightforward to use different P matrices to represent habitats of different productivity (fecundity) and mortality during the 'breeding' season.

4.3 Sex difference

Differences between sexes can be readily incorporated into Leslie Matrix models (see, eg. Fig. 16a) by assigning transfer probabilities to alternate rows and columns (eg. so that every odd row/column represents a male and every even row/column a female). It would similarly be possible to so arrange the transfer probabilities of the P matrices to achieve this. The rationale for this layout in a Leslie matrix is, presumably, that it keeps animals of the same age in pairs of rows, and age structure is a prime goal of Leslie matrices. It would however seem equally acceptable to put a block of male values together, followed by a block of female values, as shown in Fig. 16b (either lay-out would (presumably)

Figures 16. Alternative schemes for incorporating sex differences into matrix models.

Figure 16a, (from Jeffers, 1978, quoting Williamson 1959)

Model for three age classes for BOTH male and female individuals with the sexes in alternate positions on rows and columns. <u>Survival and fecundity ONLY</u>.

$$
\text{'FROM'}
$$

$$
\text{'TO'}\quad
\begin{array}{c|cccccc|}
 & F_0 & F_0 & M_1 & F_1 & M_2 & F_2 \\
\hline
M_0 & 0 & f_{m0} & 0 & f_{m1} & 0 & f_{m2} \\
F_0 & 0 & f_{f0} & 0 & f_{f1} & 0 & f_{f2} \\
M_1 & p_{m0} & 0 & 0 & 0 & 0 & 0 \\
F_1 & 0 & p_{f0} & 0 & 0 & 0 & 0 \\
M_2 & 0 & 0 & p_{m1} & 0 & 0 & 0 \\
F_2 & 0 & 0 & 0 & p_{f1} & 0 & 0
\end{array}
\quad
\begin{array}{c}
\underline{N}_t \\
\hline
n_{t,m0} \\
n_{t,f0} \\
n_{t,m1} \\
n_{t,f1} \\
n_{t,m2} \\
n_{t,f2}
\end{array}
=
\begin{array}{c}
\underline{N}_{t+1} \\
\hline
n_{t+1,m0} \\
n_{t+1,f0} \\
n_{t+1,m1} \\
n_{t+1,f1} \\
n_{t+1,m2} \\
n_{t+1,f2}
\end{array}
$$

Figure 16b. Model of Weight Changes for five weight classes, with the sexes arranged in blocks. Terms not shown are ZEROs.

FIG 16 B

KEY to symbols

♂	♀	
L	l	Loose weight
M	m	Maintain "
G	g	Gain "
B,B'	b,b'	'Born', per capita, *each* sex

Transitions

'FROM'

'TO'

		MALES					FEMALES				
CLASS NOs.		1	2	3	4	5	I	II	III	IV	V
MALES	1	M	L		B	B				b'	b'
	2	G	M	L							
	3		G	M	L						
	4			G	M	L					
	5				G	M					
FEMALES	I				B'	B	m	l		b	b
	II						g	m	l		
	III							g	m	l	
	IV								g	m	l
	V									g	m

Figure 16c. Given the lay-out of Figure 16b above, and assuming that males and females had equal numbers of male and female offspring, then the boldly outlined sub-matrices of Figure 16b could be treated as two separate sub-matrices.

Assuming the sex-ratio of the population was not changing, then the eigen values of these two sub-matrices should be the same (allowing for estimation error). This might, in these circumstance serve as a useful check of consistency for both Leslie and 'Condition' models.

(N.B. the fecundity terms B and b would need doubling to include those 'effectively from' B', b' given the notation of Figure 16b.

have the same eigenvalue). In the present context the lay-out of Fig. 16a might be more appropriate if there was no sexual dimorphism in size. The algorithms for CONTEST and SCRAMBLE competition would then only need modifying to work on alternate columns (ie. first males, then females) for transfers. It is less clear, however, how the critical threshold would be defined for CONTEST competition: presumably there should be a level for each sex, a deduction which raises two points in relation to sexually dimorphic species. First, do the outcomes of contests between individuals of different sexes depend largely on their weight irrespective of their sex and, second, if we are modelling sex differences, does the outcome of a contest of a paired individual depend solely on its own rank and that of its opponent, or do the ranks of their respective mates affect the oucome? For example Scott (1979) has shown that the ranks of both birds in pairs of Bewick's swans affect not only their own contests, but also those of their cygnets when the families are together in winter flocks. Such factors would require more complex structuring of the P transition matrix and the competition algorithms, along the lines suggested below for genetic factors.

4.4 Genetic differences between individuals

It is well known from population genetics theory that different genotypes possessed of different fecundities, mortalities, mating preference and habitat preference can lead to the maintenance of stable polymorphisms. These considerations are largely ignored by populations dynamics theory, and often in practice as well. There is however, particularly for plants, evidence for genetic 'ecotypes' that are more closely adapted to particular environments, and for vertebrates a few studies that relate fitness parameters (mortality, fecundity, growth, dispersal habits) to genetic marker alleles (allozymes), (for example: Myers & Krebs 1974, Bacon 1980, Evans 1981).

The present population model, being a compartment model, could permit inclusion of individuals of different genotypes, as described above for sex differences. Each weight class would be sub-divided into G genotypes, arranged in a standard order, with differing probabilities of weight change and different fecundity values. Such a structure imposes the restrictions that these transfer probabilities must be arranged so that any change maintains the genotype of the individual (ie. In Fig. 17a the values are in such positions that an SS individual in class 2 changes for example, to represent an SS individual in class 3 NOT an SF or FF individual in class 3, or in any other class, as illustrated).

This structure will cope with growth and mortality, but an additional sub-routine will be needed for fecundity as the average number of offspring produced by individuals of a given genotype will vary depending on the relative frequencies of the genotypes of their mates, even in a random mating population.

If mating is non-random the required structure becomes much more complex. First, we must introduce a complex sub-routine to produce suitable frequencies of the different pairs (non-random mating will impose a sexual and genetic sub-structure) and second, we are forced to explicity recognise, and incorporate into the model, the fact that fecundities are, for such species, likely to be a function of attributes of the pair not just the sum of the effects of each individual (ie. the genotype of individuals have synergistic effects on the fecundity of their mates, these effects varying with the mate's genotype; see Fig. 18).

We may perhaps conclude here that while many aspects of such a process could be conveniently summarised in a P matrix as shown in Fig. 18, the whole process cannot usually be so summarised. Accordingly a more convenient structure might be to represent the elements of Fig. 18 as separate matrices linked by appropriate sequences of algorithms, and recognise that the model is now much closer to a complex simulation model than to a simple matrix model.

Figure 17. The figure illustrates how Growth, Mortality and Competition could be fitted into a matrix format for a model of population dynamics incorporating genetic differences between individuals. The genetic types are expressed in terms of marker alleles S and F at a co-dominant Mendelian locus.

The fecundity terms are shown as *, because the production of offspring of a particular genotype, even given random mating, depends not only on the numbers of one genotype but also on the numbers of other genotypes for mating. Accordingly it would be essential in any such model to have a separate sub-routine for 'Births'.

FIG. 17

Transitions			'FROM' CLASS								
	CLASSES		CLASS 1			CLASS 2			CLASS 3		
		genotypes	genotypes			genotypes			genotypes		
			SS	SF	FF	SS	SF	FF	SS	SF	FF
'TO' CLASSES	CLASS 1	SS	M_{cg}	0	0	L_{cg}	0	0	*	*	*
		SF	0	M_{cg}	0	0	L_{cg}	0	*	*	*
		FF	0	0	M_{cg}	0	0	L_{cg}	*	*	*
	CLASS 2	SS	G_{cg}	0	0	M_{cg}	0	0	L_{cg}	0	0
		SF	0	G_{cg}	0	0	M_{cg}	0	0	L_{cg}	0
		FF	0	0	G_{cg}	0	0	M_{cg}	0	0	L_{cg}
	CLASS 3	SS	0	0	0	G_{cg}	0	0	M_{cg}	0	0
		SF	0	0	0	0	G_{cg}	0	0	M_{cg}	0
		FF	0	0	0	0	0	G_{cg}	0	0	M_{cg}

KEY
L = Loose weight
M = Maintain "
G = Gain "

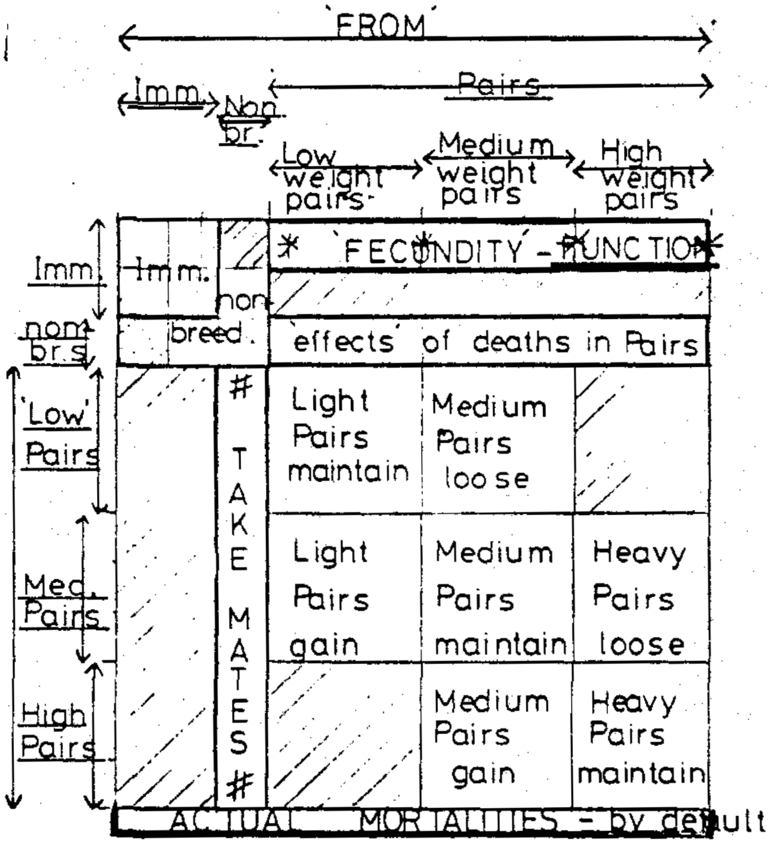
subscripts
c = Class
g = Genotype

* Fecundity: requires special treatment

Figure 18. The figure illustrates how growth, mortality and competition could be incorporated into a matrix structure and include (i) sex differenc (ii) genotypic differences and (iii) a social system where the outcome of contests depended on the combined attributes (Condition, paired status and genotype) of paired individuals.

The matrix sections labelled 'Immatures' and 'non-breeders' would be differentiated according to (a) sex and (b) genotype and would consist of sub-elements with terms on the diagonals of each sub-element only to preserve sex and genotype during transitions, as shown in Figure 17.

The matrix sections labelled 'Pairs' would correspond to combinations of male and female genotypes in pairs and categorised according to their combined weight/status.



Imm. = immatures
Non-br. = non-breeders

* Fecundity } require speial
\# Take mates } sub-routines

As in Figure 17, fecundities and breeding require species treatment. In this instance the most appropriate treatment would be a subroutine to allow appropriate matings to 'take place', depending on the frequencies of potential mates of different genotypes and any genotypic mating preferences. Thereafter, fecundities could be assigned as proportions of overall average family size as dictated by classic Mendelian ratios.

A species case is introduced by deaths within pairs, where the death of one paired member creates a widow/widower: this can be accounted for as shown.

4.5 Energetics and resource allocation

4.5.1 Energetics

In previous sections dealing with constrained population growth we have considered the population to be limited with respect to environmentally available food and have enumerated this limitation in terms of 'equivalent animal biomass maintainable by food resources', K.biomass. We further made the simplifying assumption that the energy from one unit of food would maintain one unit of body mass irrespective of body size, whereas metabolic rate varies logarithmically with size (see, eg. Southwood 1981), transport energy requirements, and hence foraging costs, will also vary with size and the energy requirements of producing offspring will obviously vary with the number, and size, of offspring produced. There are good grounds therefore for enumerating our limitation in units of energy rather than biomass, and we can envisage doing this as shown in Table 5. Just as we can envisage a typical weight for members of classes 1C, so we can envisage typical energy requirements for maintaining those weights under 'field' conditions, as shown in the column headed E1 in Table 5. These energy requirements could clearly be used, in combination with a value for 'total energy available from habitat', say K.energy, as a basis for limiting the population, in a manner directly analagous to the models of sections 3.3 to 3.5 (and the programs LOMNOC.BAS, LOMUO3.BAS and LOMSR2.BAS). Such a model would retain the assumption that the limiting factor, now energy, was not limiting during the period of offspring production and, accordingly, the fecundity values would not vary with population size.

4.5.2 Fecundity limited by energetics

Contrary to the above simplifying assumption it would, for many species, be more realistic to assume that energy requirements may limit the number of offspring that an individual, or pair, can produce (at some defined stage, such as egg laying in insects, egg laying or fledging in birds, birth or weaning in mammals). The energy budget for rearing offspring

TABLE 5: The table illustrates how energy requirements for body maintenance, E1, and reproduction, E2, could be assigned to individuals of each class, 1-5, having weights typical of their class (ie. within the class limits).

The overall energy requirements, E3, could be used to constrain population growth in a manner analagous to the use of the 'biomass limit' (K.biomass) of the previous examples. Different partitioning of this energy need (body growth and maintenance versus reproduction) could be investigated to determine 'optimal' partitioning in defined circumstances.

		E1		E2	E3
CLASS NO.	Typical body weight	Energy required for maintenance	Typical fecundities	Energy required for rearing offspring	Total energy needs
1	5.0	100	0	0	100
2.	5.5	110	0	0	110
3	6.0	115	0	0	115
4	7.0	130	4.5	45	175
5	8.5	150	5.5	60	210

could be drawn up as in Table 5, which recognises (column <u>E2</u>) that the cost of producing additional offspring may be greater than the cost of producing the initial ones (due to increased foraging distances, etc.). We may now think of extending the model in terms of <u>Resource</u> <u>allocation</u>. In relation to our seasonal model (section 4.1) we envisage the classes of the matrices as representing differing amounts of energy that individuals can expect to <u>monopolise</u>, either by accumulating these resources within themselves (fat, eggs, etc.) or by defending territories that contain that amount of energy resource. Extending the model further along these lines, we should be able to address the problem of energy/resource partitioning. Within physiological limits, an individual having access to a set limited amount of resource can use it for two basic purposes, growth or reproduction. Lack (1954) and Perrins (loc. cit.) argue convincingly that the clutch size of a species should be selected to that which, on average, leaves the most surviving offspring. It is widely recognised however that, given seasonal variation, age and condition dependent mortalities, habitat and individual variability, the optimal choice of partitioning for an individual is far from clear, particularly if rearing many offspring decreases the parents' condition and survival prospects. Hence, if within our 'Resource monopolisation' classes we assume several different types of partitioning strategy (growth vs. reproduction) and assign to these realistic values of heritability, we could investigate not only the optimal 'clutch' size in different circumstances but also the effects of different amounts of (seasonal) environmental variation on the expected variance of clutch size (we would require additional sub-routines to cope with the complexities of periods of parental care). There is one important practical difference between this suggestion and the seasonal condition model of section 4.1, namely that food availability (K.biomass) is notoriously hard to estimate. Energy usage can, on the other hand, be measured accurately (Bryant) though the techniques are fairly complex. While it would also be very difficult to estimate 'energy availability' it may be possible, by experimental manipulations, to estimate the increasing energy costs, and net energy gain, to broods of differing sizes, eg. Figure 19.

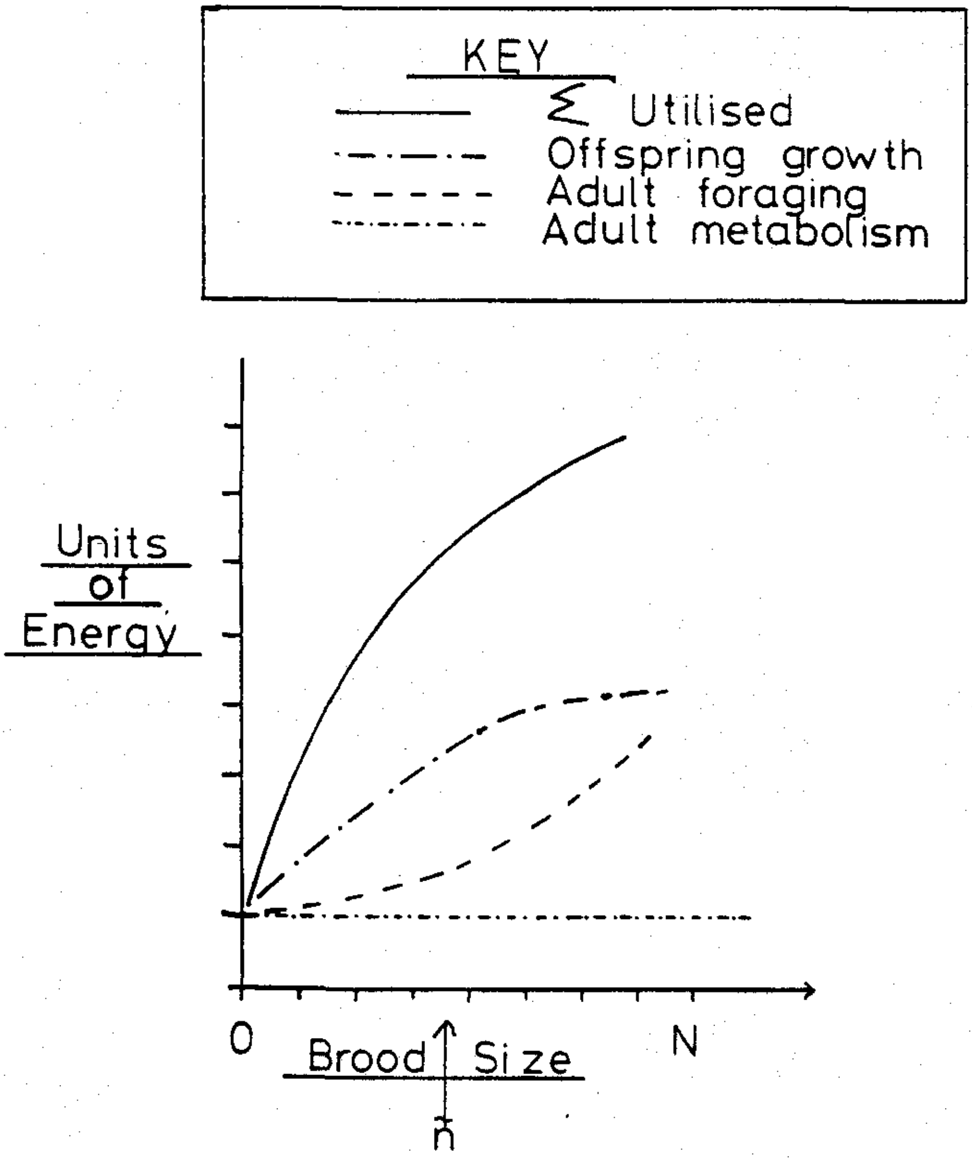
Figure 19. The Figure illustrates the way in which Total Utilised energy might change depending on the size of brood being reared by a breeding pair.

Adult basal metabolism will stay roughly constant, but adult travelling energy will increase as brood size increases, as more and further foraging trips will be required to provision the brood.

Energy utilised by the brood will rise with brood size, but as brood size exceeds that with which adults can readily cope the utilised energy will drop off below the idealised offspring DEMAND, which would be linear with brood size.

Accordingly, a curve could be constructed (Utilised) of the total energy the family was able to utilise. The optimal breeding strategy is a trade-off between Brood size, energy costs and survival prospects for brood and adults.

FIG. 19



4.6 Disease and debilitation

It has long been recognised that prey-predator and host-pathogen interactions play important roles in the population dynamics of some species. The types of effect produced by different pathogens have recently been investigated mathematically (eg. Anderson & May 1979 a,b). In Section 4.7 I briefly outline how a prey-predator 'condition' model could be devised whereas in this section I suggest a means whereby the sub-lethal, or debilitating, effects of diseases might be investigated.

It is logical to divide the host population into types, which is facilitated by the structure of a compartment model. These types would be (i) healthy, uninfected individuals (ii) infected individuals incubating the disease (iii) infected and infectious individuals showing symptoms of disease and capable of transmission (iv) immune individuals. These divisions are similar to those of Anderson & May 1979a and can be illustrated as shown in Fig. 20 (compare this figure with Anderson & May's (1979 a) Fig. 3).

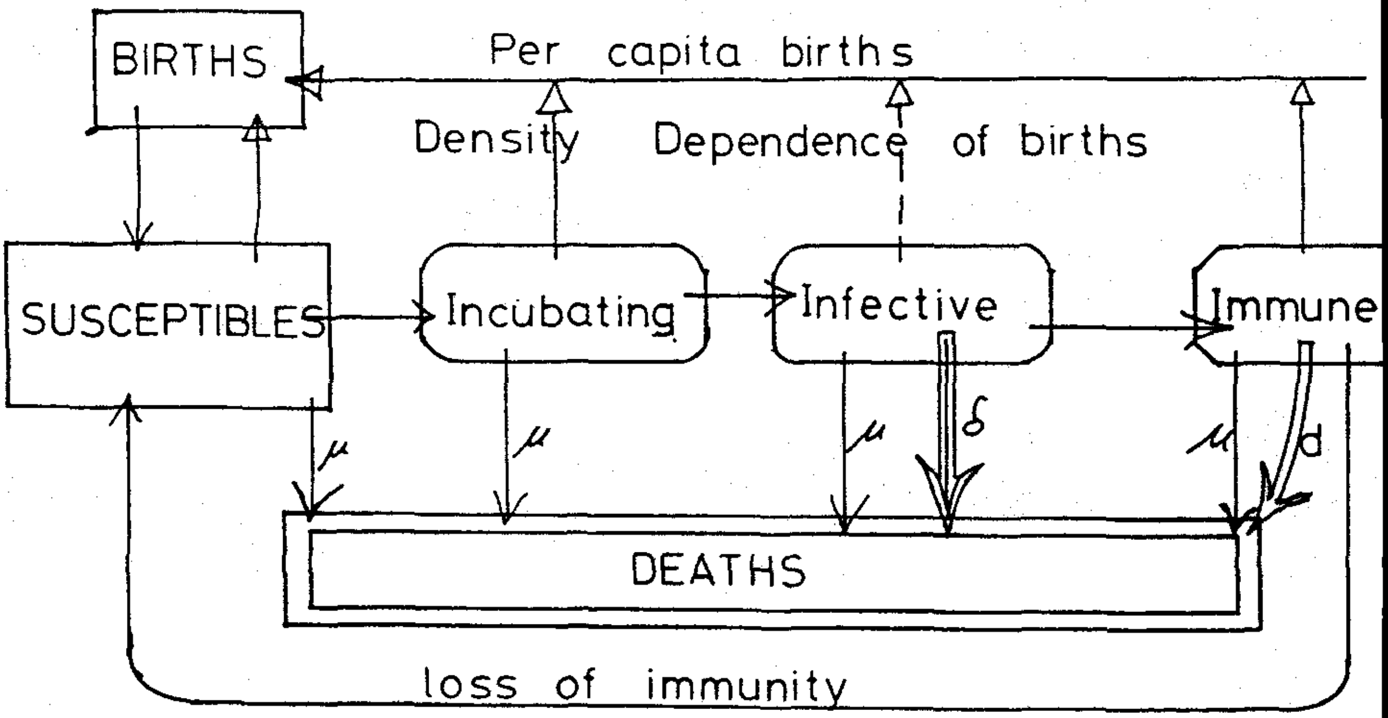
The differential equations used by Anderson & May 1979 to describe the processes of Fig. 20 carry the assumption that the various stages take place in the same (vanishingly small) unit of time, that the effects are the same for all members of an epidemiological class, and that the per capita birth rate is the same for all epidemiological classes.

We illustrate the way a compartment model could be structured to describe epidemics in Figure 21. In both of these diagrams there is an implicit assumption (which could be relaxed by appropriate extra sub-routines during simulation) that infection probability is independent of host density, but we emphasise that this restriction could easily be relaxed and applies only to the matrices shown in the figure. Both parts A and B of Fig. 21 assume a structure for uninfected populations as shown by the boldly outlined 3 x 3 sub-matrix. In Fig. 21a we assume a hypothetical disease that is very debilitating, (over a variable period and with variable severity) and a negligible period of immunity. In Fig. 21a the probabilities: i_{ij} represent the probabilities that individuals from

Figure 20. Schematic representation of the main epidemiological classes that may need to be distinguished for a generalised disease. The arrows represent transfers of individuals from one class to another during population dynamics and the course of the disease.

Depending on the nature of a particular disease the letters shown might be constants or functions of other variables.

FIG. 20



KEY
μ mortality from natural causes (density dependent
δ direct mortality 'caused' by disease
d 'dibilitation' induced death [density dependent]

Figure 21a. Debilitating disease model with probalistic recovery to 'full health' over a variable period of time, including competition effects.

FIG, 21:A

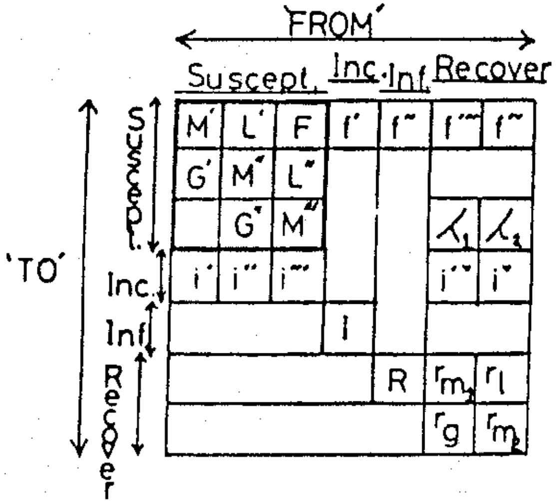
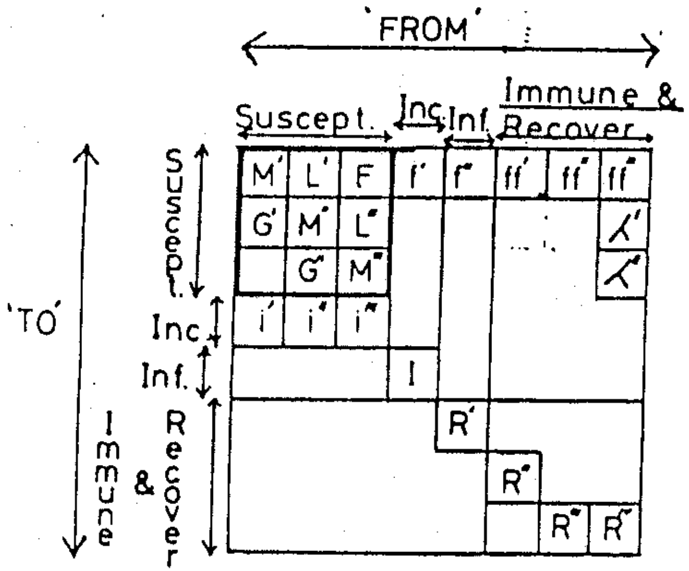


Figure 21b. Immunity model with progressive recovery over a set minimum period of immunity, followed by reversion to susceptibility.

FIG. 21:B



KEY: The letters within the matrices refer to array elements or sub-matrices of the model, depending on whether or not the model is envisaged to be sub-structured for sexual or genetic differences. '' indicate similar concepts for the value(s) but varying values in each case.

M = Maintain weight
G = Gain weight
L = Loose weight

F, f, ff = Fecundity terms (see text)

i = infection prob./function
I = survival to infectious prob.
R = recovery from infection
r_l, r_m, r_g = condition maintenance/loss/gain probabilities during recovery
λ = reversion to susceptibility, (or 'recovery' in Figure 21a).

class i will become infected; the probability I_{ij} that an infected individual will survive to become infectious; R_{ij} the probability than an infected individual will survive into a low weight class of debilitated survivors; rm, rg, rl, rm the probabilities that debilitated survivors will survive and maintain, lose or gain weight (the disease may have made them more susceptible to other infections, etc.), and λ_{ij} the probabilities that recovering debilitated individuals will recover completely. The f_{ij} represent fecundities of 'diseased and recovering' individuals, with the expectation that $0 \leq f_{ij} < F$ for all ij.

In Fig. 21b we assume another hypothetical disease which is debilitating in its initial stages, but has progressive recovery over a fairly long period of immunity. The symbols are as for Fig. 21a, with the exceptions: rm, rg and rl are omitted, as recovery is systematic; the R_{ij}s represent the survival of immunes and, in the form shown, impose a time delay between onset of immunity and reversion to susceptibility (λ); the f_{ij}s and ff_{ij}s represent fecundities with the expectations $0 <= f_{ij} < F$ and $F > ff_{ij} \fallingdotseq F$.

The matrix structures shown in Fig. 21 would be adequate for simple purposes, although the algorithms for CONTEST competition would clearly be different, and would need to be separately written for each such application (as the 'weights' are no longer in rank order throughout the matrix). It should be stressed here that, for the example of Fig. 21b, CONTEST competition could affect the basic dynamics between the host and pathogen. This will occur when the disease debilitates individuals to an extent that they become very low in the social hierarchy and likely to lose weight and starve: in these circumstances mortality of immune individuals would be increased, the extent of this increase depending on current environmental factors as well as host population level.

4.7 Prey-predator models

The essence of prey-predator models is to write two or more equations (or link two or more simulation routines) such that one equation/simulation describes the behaviour of the prey population, preferably in a resource limiting environment and incorporating the effects of predation on the prey, while the second equation models the behaviour of the predator with the results from the prey equation being used to describe the resource (=food) limitations on the predator population. Classically there are the prey-predator equations due to Lotka and Volterra and elaborated by Leslie and others (for examples see Smith 1974) and some of the more complex elaborations include age structured populations.

In the case of 'condition' models it is clear that the simulations described in sections 3.4 and 3.5 could be used to describe the behaviour of a 'prey' species in a resource limiting environment and the outputs of this used to indicate the prey resources available to the predator. A predation subroutine could then be added to account for the interactions, and such a subroutine should:-

i. allow preferential predation by the predators on the less fit classes of the prey population

ii. for a mobile predator use a 'catch per unit effort' curve to assess net weight gains/losses to predators at different prey densities due to different searching efforts required to find prey at those densities.

5 TESTING THE 'CONDITION' MODEL

5.1 Facilities for 'captive' experiments

The model relies on having frequent weighings of identifiable individuals in relation to a known food supply. For these reasons it would be efficacious to monitor a 'laboratory' or confined population which relied on food supplied by the experimenter. Such an approach would not only allow the experimenter to know (estimate accurately) K.biomass, but also to vary the actual levels of K.biomass, corresponding to seasonal changes, and record the effects of this. It is important to note that such an approach would enable the experimenter to determine the values of the P matrix (probabilities and productivities) for a population having super-abundant food, as the model envisages, and then to observe the effects on numbers and condition as the population approached carrying capacity and competition began to have a large effect.

The assumptions of the model could be tested by observing competitive interactions, and its predictions by comparing weight distributions and weight/age distributions.

5.2 Field experiments

Laboratory tests as outlined above are convenient, but run the risk of being done under abnormal conditions where important natural regulatory mechanisms may not operate correctly. While it is easy to envisage a field study that could estimate the values required for the P matrix (choice of suitable study species would be important) it must be recognised that such values would often refer to a population already limited by competition: accordingly, the effects of the 'competition' algorithm would be greatly underestimated, as much of their effect would be hidden in the 'probabilities of random weight loss' values in the P matrix.

It is likely, however, that suitable field experiments could be devised for some species. These would, ideally, involve the use of large enclosures (to prevent immigration from obscuring the results) plus 'removal' and 'supplementary feeding' experiments. The former would be undertaken to reduce the population level to well below K, thus allowing estimates of the $\underline{P}$ values to be made as the population recovered towards K. The latter would allow similar estimation of $\underline{P}$ values as the population rose from the 'natural' K to the 'K-supplement' level and would also permit monitoring of the severe competition that would result when the food supplement was curtailed.

5.3 'Natural' field data

It would be perfectly possible to construct a population model based on $\underline{P}$ values estimated direct from field data but, as explained above, such procedure would very likely grossly underestimate the effects of competition unless it were possible to determine whether deaths and/or weight losses were due to (i) chance factors or (ii) competitive exclusion. Such discrimination seems optimistic, but might be possible for some species: for example Krebs et al (eg. Myers & Krebs, loc. cit.), have shown that the frequency of 'rump-wounding', caused by aggressive conflicts, rises in high density vole populations and it might be possible to use such scars as indicators of 'chance' versus 'competitive' causes of weight loss and starvation.

5.4 Algebraic and sensitivity analysis

While these models use matrices for convenience it must be clearly understood that the processes involved are not described by standard mathematical matrix operations only, at least when population growth is constrained by competition. However, algebraic analysis of similar complex models based on matrices have been enlightening, particularly when done in concort with simulation and sensitivity analysis (see, eg. the review by Usher 1972).

I suspect that algebraic analysis could give some insight to the advantages and pitfalls of the current models, though it would require a mathematical expertise which I do not personally have. I would further suggest that a particularly important aspect for such an algebraic study would be the interaction of terms of different relative magnitudes between and along the three diagonals of the P matrix. It would be appropriate at this point to mention that the probability values used on the diagonals of the example data matrices for this paper were chosen after some careful thought. It would clearly be possible to insert (mathematical) values that would promote instability rather than stability. In most cases stability would be more 'desirable' ecologically and it would be most interesting to compare the structures of P matrices estimated from field data with those which, mathematically, give greater stability and resilience. I suspect these rules might be fairly simple, as the example data set used here represented my first attempt at inventing a suitable arrangement and it did not produce wildly unrealistic results.

Sensitivity analysis of such models would clearly be desirable, in particular to investigate the effects of minor variations in the 'weight change' probabilities and the fecundity values. This should be done both in relation to variations in absolute values and the relative structures of those values. However, in view of the great plethora of values and structures that could be theoretically envisaged I do not think such investigation could usefully be carried out without some 'first order' approximations to actual values derived from field data.

6 SUMMARY

ch.2 A brief historical survey of mathematical models of population dynamics is given, including differential equations, difference equations and Leslies matrices. It is suggested that a fundamental flaw in these approaches is their implicit assumption that all individuals in a population are phenotypically identical. Lomnicki's findings that population dynamics can be greatly affected by individual differences, habitat heterogeneity and social hierarchies are stressed. The sparsity of data used in many population dynamics models is commented on (eg. models 'validated' by comparing observed and model predictions of time-series of numbers only) and the question is raised as to whether such simple comparisons will permit discrimination between equally 'good' (or equally 'poor'!) models.

ch.3 A model of population dynamics based on numbers of individuals in different 'condition' classes is developed. It is assumed that body weight, 'condition', social dominance and fecundity will vary between the classes and, in these simple initial models, that dominant individuals will be in 'good condition', have higher body weights and higher fecundities. In discrete units of time individuals may: (i) either die, starve, lose weight, maintain weight, gain weight and (ii) reproduce with varying fecundities. These assumptions lead to stable ratios of 'Numbers per Weight Class' in the population; except for an unstable equilibrium, the population size increases or decreases exponentially.

The above model is modified to include two algorithms that regulate the population by competition for limited food resources, K_F. The two algorithms correspond to the concepts of 'Scramble' and 'Contest' competition for resources. These algorithms are based on biologically likely assumptions and do not depend on mathematically arbitrary formulae for density dependent changes in fecundity or mortality. It is shown that these new models of population growth in a constraining environment (food is limited) lead to stable levels of 'numbers of individuals per weight class'; these stable levels have different ratios of one class frequency to another for the two types of competition.

The above models are extended to investigate the effects of varying the absolute amounts of 'available food', K, from one time period to the next. Results indicate that, for the range of parameters used, populations controlled by 'Contest' competition are more able to cope with extreme environmental variation than are 'Scramble' controlled populations.

ch.4 Outlines are given for extending this type of model to cope with more complex and more realistic ecological situations, including:

- seasonal pattern of food availability
- habitat heterogeneity and dispersal
- sex differences in survival, fecundity, etc.
- genetic differences
- energetics and resource allocation
- diseases, including sub-lethal effects

ch.5 The merits of different ways of collecting data to test the model are briefly discussed. The potential for algebraic analysis of the model's matrices is considered and the main aims for sensitivity analyses of the simulation models are suggested.

7 CONCLUSIONS

The simulations presented here support Lomnicki's suggestions that population regulation can be achieved by constructing models based on biologically meaningful rules and assumptions without the need to involve fairly arbitrary mathematical functions to coerce the model into stable (or cyclic) behaviour. While such models may be difficult to analyse mathematically it is suggested that their construction is likely to prove enlightening to both field ecologists and biometricians. Eventual testing of such models will depend on the collection of suitable sets of experimental data.

8 ACKNOWLEDGEMENTS

The ideas underlying the models described in this paper have developed slowly, around several disparate topics, over several years. During this time my thoughts have been aided and clarified by numerous discussions with colleagues from the Zoology Departments of Birmingham and Oxford Universities (particularly members of the Edward Grey Institute and Animal Behaviour Research Group at Oxford) and at the various research stations of the Institute of Terrestrial Ecology. I am grateful to O.W. Heal, J.N.R. Jeffers and I. Newton for their constructive criticisms of an earlier draft. Finally, I would like to thank Miss Tracey Pyers for her prompt, efficient and cheerful work on the typing and preparation of the drafts of this paper.

9 REFERENCES

ANDERSEN-HARILD, P. 1980. Weight changes in Cygnus olor. In: Proc. 2nd Int. Swan Symposium, Sapporo, Japan, 359-378. Slimbridge: International Waterfowl Research Bureau.

ANDERSON, R.M. & MAY, R.M. 1979. Population biology of infectious diseases: Part I. Nature, Lond., 280, 361-367.

BACON, P.J. 1980. Population genetics of the Mute swan (Cygnus olor). D. Phil. thesis, University of Oxford.

BACON, P.J. 1981. Population genetics of Cygnus olor. In: Proc. 2nd Int. Swan Symposium, Sapporo, Japan, 1980, 389-394. Slimbridge: International Waterfowl Research Bureau.

BACON, P.J. 1981. A stochastic matrix model of macrophyte growth and competition on the river Lambourn. NERC contract report to Freshwater Biological Association. (unpublished).

BEDDINGTON, J.R. 1975. Economic and ecological analysis of red deer harvesting in Scotland. J. environ. Manage., 3, 91-103.

BRYANT, D.M. 1979. Reproductive energetics of a free-living bird. J. Anim. Ecol., 48, 471-482.

DORF, R.C. 1969. Matrix algebra: a programmed introduction. London: Wiley.

EVANS, P.G.H. 1981. Population genetics of the European starling (Sturnus vulgaris). D. Phil. thesis, University of Oxford.

GALE, J.S. 1980. Population genetics. London: Blackie.

JEFFERS, J.N.R. 1978. An introduction to systems analysis: with ecological application. London: Edward Arnold.

LACK, D. 1954. The natural regulation of animal numbers. Oxford: Clarendon.

LESLIE, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika, 33, 183-212.

LESLIE, P.H. 1959. The properties of a certain lag type of population growth and the influence of an external random factor on such populations. Physiol. Zool., 32, 151-9.

LESSELLES, K.M. 1975. Spring flock structure of the Mute swan (Cygnus olor). B.Sc. Hons. project, Department of Zoology, University of Oxford.

LOMNICKI, A. 1978. Individual differences between animals and the natural regulation of their numbers. J. Anim. Ecol., 47, 461-475.

LOMNICKI, A. 1980. Regulation of population density due to individual differences and patchy environment. Oikos, 35, 185-193.

MacARTHUR, R.H. 1972. Geographical ecology. New York: Harper & Row.

MacDONALD, D.W., BUNCE, R.G.H. & BACON, P.J. 1981. Fox populations, habitat characterisation and rabies control. J. Biogeogr., 8, 145-151.

MYERS, J.H. & KREBS, C.J. 1974. Population cycles in rodents. Sci. Am., 230, 38-46.

NEWTON. I. 1972. Finches. London: Collins.

PAULY, D. & DAVID, N. 1980. An objective method for determining fish growth from length-frequency data. ICLARM Newsletter, 3 (3), 13-16.

PERRINS, C.M. 1970. The timing of bird's breeding seasons. Ibis, 112, 242-255.

REYNOLDS, C.M. 1972. Mute swan weights in relation to breeding. Wildfowl, 23, 111-118.

SCOTT, D.K. 1978. Social behaviour of wintering Bewicks' swans. Ph.D. thesis, University of Cambridge.

SMITH, J.M. 1974. Models in ecology. Cambridge: Cambridge University Press.

SOUTHWOOD, T.R.E. 1981. Bionomic strategies and population parameters In: Theoretical ecology: principles and applications, edited by R.M. May, 30-52. Oxford: Blackwell Scientific.

USHER, M.B. 1966. A matrix approach to the management of renewable resources, with special reference to selection forests. J. appl. Ecol., 3, 355-367.

USHER, M.B. 1969. A matrix model for forest management. Biometrics, 25, 309-315.

USHER, M.B. 1972. Developments in the Leslie Matrix Model. In: Mathematical models in ecology, edited by J.N.R. Jeffers, 29-60. Oxford: Blackwell Scientific.

WILLIAMSON, M.H. 1967. Introducing students to the concepts of population dynamics. In: The teaching of ecology, edited by J.M. Lambert, 169-175. Oxford: Blackwell Scientific.