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# "Structured population models: a tool for linking effects at individual and population level"

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# Structured population models: a tool for linking effects at individual and population level

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We address the problem of relating information on the effects of a particular stress on *individuals* to possible effects at the *population* level. Structured population models aim to predict population dynamics from a careful specification of the dynamics of individuals; however, in spite of major mathematical advances, there are only a few cases where such models have made significant contributions to ecological understanding. This paper reports progress to date on a project in which we construct both individual and population models of *Daphnia*. We present a model of individual growth and development which has been tested against results from several laboratories on *D. pulex*. We propose a simple, stage-structured population model and give a preliminary report of some of its properties.

KEY WORDS:—Structured population model – population dynamics – *Daphnia* energy allocation – population cycles.

CONTENTS

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## INTRODUCTION

One fundamental impediment to elucidating the concept of stress in ecology is that the simplest measurements to undertake are often on *individuals*, while our primary interest is likely to be in effects at the *population* level. For example, the direct effects of toxic substances may be to inhibit growth or development, reduce fecundity or increase mortality; the consequent changes in population densities and in the pattern of population fluctuations depend on the regulatory mechanisms of the population under investigation. It follows that a potentially valuable tool in the study of ecological stress will be *structured population models* which aim to predict the dynamics of a population, given a well-posed, dynamic specification of the response of individual members of that population to external factors.

Systematic mathematical methods for the formulation and analysis of structured population models have been developed in recent years (e.g. Metz & Diekmann, 1986), but there has been much less progress in the equally demanding task of assessing their practical utility. The appropriate level of complexity of a model for a particular task remains a matter of considerable controversy, progress towards whose resolution would be considerably assisted by some detailed case studies. We therefore have started a programme in which we plan to contrast the performance of simple and complex models of the zooplankter *Daphnia*. These animals are particularly appropriate for this work as there exists a vast body of literature on the physiology of stressed and unstressed individuals as well as data on laboratory and natural populations.

Many natural *Daphnia* populations exist at low food levels, sustained by a balance between low fecundity and (presumably) mortality. Two of us (Murdoch & McCauley, 1985; McCauley & Murdoch, 1987; McCauley, Murdoch & Watson, 1988) have previously conjectured that the diverse patterns of *Daphnia* dynamics that follow a spring algal peak reflect the *Daphnia*–food interaction rather than exogenous forcing by biotic or abiotic factors. If these conjectures are valid, it follows that any model of *Daphnia* population dynamics must treat carefully the assimilation and utilization of food.

McCauley & Murdoch (1987) also showed that quasi-cyclic fluctuations in both laboratory and field populations of *Daphnia* have a dominant period close to the generation time and (where demographic data are available) that the fluctuations have the following pattern: a burst of reproduction at low density producing a peak population consisting largely of juveniles, then a long period of declining density, suppressed reproduction, and slow juvenile development, the population at its nadir consisting largely of adults which eventually produce the next burst of recruits. These observations support our premise that a realistic population model must incorporate some aspects of the physiological structure (e.g. proportions of large/small, old/young individuals) of the population.

As already noted, development of such a structured population model starts with the construction of a model of the properties of individuals, and in previous

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papers (McCauley *et al.*, 1989b; Gurney *et al.*, 1989) we developed one such model for *Daphnia*. For a detailed exposition we refer the reader to Gurney *et al.* (1989), but its main assumptions are set out in section 2 of the present paper. The emphasis of that section is on the judgements that were necessary to construct the model and not on the technical details. In similar spirit we refer the reader to the original paper for detail of our quantitative tests of the model, but highlight certain qualitative predictions on starvation and recovery, an area where the model suggests new critical experiments.

In section 3, we discuss the problems inherent in constructing a population model based on our rather elaborate description of individual physiology, and we expose certain formidable technical obstacles that preclude immediate incorporation of our model within the standard mathematical framework for structured population models. To circumvent these problems, which are the subject of current research, we simplify our description of individual physiology, so as to permit development of a model in which the population dynamics are described in terms of a set of coupled delay-differential equations. Quantitative tests of the model are still in progress, but we discuss its ability to explain the demography of the cycles in real *Daphnia* populations.

## A MODEL OF GROWTH AND REPRODUCTION IN INDIVIDUAL DAPHNIA

The model developed in our two previous papers (McCauley *et al.*, 1989b; Gurney *et al.*, 1989) describes dynamically the utilization of food by daphnids for growth, maintenance and reproduction; for this we need a description of 'food'. Notwithstanding evidence that the composition of the algal population, and in particular the edible fraction, may significantly influence *Daphnia* population dynamics (McCauley *et al.*, 1988 and references therein) we initially regard food as a homogeneous assemblage within the water, describable by a single density, namely carbon content per unit volume. The model describes the fate of this carbon following ingestion, and specifies a set of 'sinks' or 'pools' within a daphnid, together with a set of rules for allocating assimilate to these pools. The model equations are summarized in Table 1.

### *(A) The model structure and equations*

#### *Reserves and the short-term fate of assimilate*

There is good evidence (e.g. radioisotope studies of Lampert (1975)) that assimilate is incorporated into the body structure within a few hours, so we do not need a representation of short-term reserves in the model. There is also good evidence from starvation experiments that as much as 70% of body tissue may be used as long-term reserves during periods of starvation. We therefore assume that (long-term) reserves constitute a specified fraction of the normal body weight (excluding eggs) of a well-fed animal; an animal dies of starvation if its body weight drops below the appropriate fraction of the 'normal' weight (defined later).

In our new energy channelling scheme (Fig. 1), we assume that assimilate is committed *immediately and irreversibly* to reproduction, or to growth and maintenance. We then assume that given 'sufficient' food, an animal of length L

TABLE 1. The model of individual growth and reproduction as specified by Gurney *et al.* (1988). The equations are set out in a style close to that required for computer implementation of the model. The symbol ← means 'is assigned the value'

| | |
|---|---|
| Food assimilation and utilization | $I_{max} = SL^{Q}[1 - \exp\{-(L/L_u)^{i}\}]$<br>$I = I_{max}F/(F + F_h)$<br>$A = \varepsilon_A I$<br>$A_{max} = \varepsilon_A I_{max}$<br>If $L < L_m$ then $K_u = 1.0$<br>else $K_u = K_{min}(A_K + 1)/(A_K + A/A_{max})$<br>If $K_u < 1.0$ then $K_o(L, A) = K_u + (1 - K_u)\exp\{(L_m - L)/L_s\}$<br>else $K_o(L, A) = 1.0$ |
| At moult | $E_{max} = T_m[1 - K_o(L, A_{max})]\varepsilon_A I_{max}$<br>$W_c = W_{co} + W_{cs}E/E_{max}$<br>If $E > W_c$ then $\{N_{ed} \leftarrow E/W_c, E \leftarrow 0\}$<br>else $\{N_e \leftarrow 0$, E unchanged$\}$<br>If $W > (L/X)^P$ then $\{L \leftarrow XW^{1/P}\}$<br>else {L unchanged} |
| Between moults | $M = BW^{Y}$<br>If $A < M$ or $W < (L/X)^P$ then $K = 1.0$<br>else $K = K_o(L, A)$<br>$dN_e/dt = dL/dt = 0$<br>$dE/dt = (1 - K)A$<br>$dW/dt = KA - M$ |
| Food dynamics | Semichemostat: $dF/dt = D(F_r - F) - I/V$<br>Transfer $dF/dt = -I/V$ between transfers<br>$F \leftarrow F_r$ at transfers |

allocates a constant proportion of assimilate to reproduction and the remaining fraction to growth and maintenance combined.

### *The utilization of assimilate when food is scarce*

We need rules for energy channelling when food supply varies as well as when it is constant. Following Kooijman (1986a, but noting that he was modelling commitment from a reserve pool and not the immediate fate of assimilate), a natural assumption is that if the default allocation of assimilate to growth and

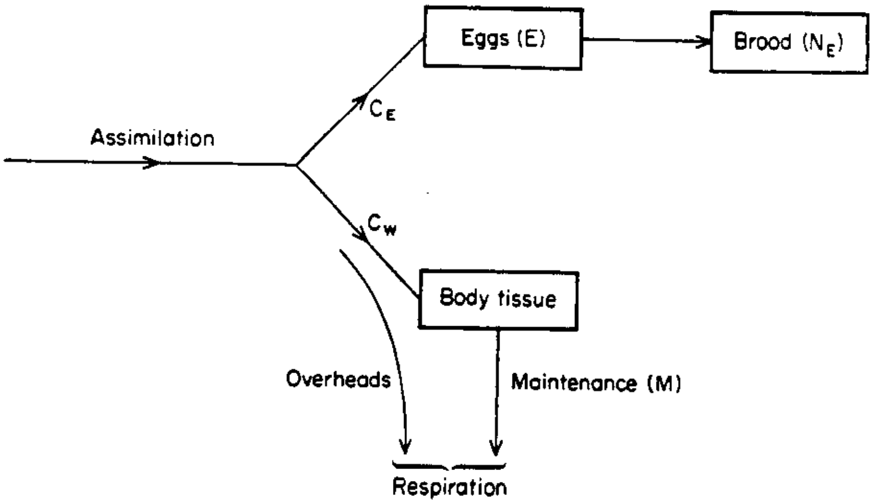

Figure 1. The energy allocation scheme in the model of individual growth and reproduction (from McCauley *et al.*, 1989b).

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maintenance is at any time insufficient to meet maintenance, then a daphnid meets immediate maintenance needs by (in order): (i) stopping growth, (ii) supressing commitment to new eggs, (iii) metabolizing reserves. However, although qualitatively plausible, a model embodying the strict priorities outlined above made predictions inconsistent with experiments on the growth of individuals in continuous flow systems, and it appears that at moderately low food densities daphnids give slightly higher priority to growth than is implied by the above rules (Gurney *et al.*, 1989).

In addition, *Daphnia* is able to recover from periods at low food levels and eventually perform at a higher food level at the same rate as individuals raised continuously at that higher level (Ingle, Wood & Banta, 1937; Kooijman, 1986a). We therefore hypothesize that starving individuals give priority to growth over reproduction whenever their weight is less than a notional 'weight-for-length'. We assume that this weight-for-length is the weight of the body (but not the eggs) of a healthy daphnid of length L immediately after the moult, there being experimental support for the existence of a simple allometric relationship between these quantities. We are thus introducing a practical criterion to define a starving animal, and then postulating that starving animals suppress reproduction in favour of recovering body weight (i.e. reserves). If the appropriate weight-for-length is reached, the normal allocation rules apply.

### *The rules for energy channelling*

We now define the variables for our model and specify the set of mathematical rules governing the utilization of assimilate by the animal.

We recognize that *Daphnia* development proceeds through a series of discrete instars separated by moults. We assume that instar duration is a constant ($T_m$) for all instars and at all food levels (though both of these assumptions can be relaxed without prejudice to the structure of the model).

We characterize a daphnid of age a by the following five *state variables:* carapace length (L), body weight excluding eggs and material destined for eggs (W), weight-for-length ($W_{fl}$) as introduced in the previous subsection, material in the body committed to egg production (E), and number of eggs in the brood pouch ($N_E$). We assume (section B) that for well-fed daphnids, weight and length are related immediately after a moult by an allometric relation of the form

$$W = (L/X)^p, \tag{1}$$

where X and p are constants.

Assimilate is assumed to be allocated between growth, reproduction and maintenance in accordance with the scheme shown in Fig. 1, where we also introduce notation for the various material fluxes. With this partitioning, elementary book-keeping yields the following differential equations which are assumed to hold ***throughout an intermoult***:

$$dW/dt = C_w - M, \tag{2}$$

$$dE/dt = C_E. \tag{3}$$

We assume that length cannot change during an intermoult, implying a similar property for $W_{fl}$. Since eggs are only released at a moult, $N_E$ cannot change during an intermoult.

*At a moult*, all the state variables except W take new values as follows:

$$L = XW^{1/p}, \tag{4}$$

unless this would produce a *decrease* in length, in which case the value of L is unchanged. The new weight-for-length is then calculated from the new length as

$$W_{fl} = (L/X)^{p}. \tag{5}$$

All assimilate committed to reproduction during the previous instar is passed as new eggs to the brood pouch (the existing clutch being released as neonates). We assume that a certain quantity of assimilate ($W_e$), whose value depends on the amount of material available for egg production, is required to produce an egg; thus the new brood size is given by

$$N_E = \begin{cases} E/W_e \text{ if } E > W_e \\ 0 \text{ otherwise} \end{cases} \tag{6}$$

where

$$W_e = W_{eo} + W_{es}E/E_{max}. \tag{7}$$

For simplicity, present implementations of the model allow fractional eggs to be passed to the brood pouch, but in principle equation (6) could be replaced by a more elaborate rule in which an integer number of eggs are passed to the brood pouch with the remaining egg material retained in the body for the next instar (as is done if there is insufficient material for even one egg). However, given the large observed variability in brood size, even for *Daphnia* grown under controlled conditions, such elaboration would appear rather unnecessary—hence the simple form for equation (6). With this simple form, the animal normally starts the next moult with no carry-over of egg material; at the start of each instar we set $E = 0$, unless the brood pouch is empty ($N_e = 0$) in which case we leave E unchanged.

Dynamically, the key feature of the model is the 'K-switch' in Fig. 1 which determines the fluxes $C_E$ and $C_w$. We define this quantity K (which is the fraction of assimilate that goes to growth plus maintenance, leaving the fraction $1-K$ for reproduction) by writing the fluxes formally in the form

$$C_w = KA, \qquad C_E = (1-K)A, \tag{8}$$

(where A is the rate of assimilating food), so the specification of the model *structure* is complete once we select the rule for calculating the quantity K. We have already noted that this allocation function must depend on length (to distinguish juveniles from adults), assimilation rate (to meet maintenance when food is scarce), and weight-for-length (to give priority to growth in animals recovering from starvation). After considering a variety of forms (Gurney *et al.*, 1989), we concluded that the structure of these dependences was given by the rule

$$\begin{aligned} &\text{If } A < M \text{ or } W < (L/X)^{p} \text{ Then } K = 1.0 \\ &\qquad\qquad\qquad\qquad\qquad\qquad \text{Else } K = K_o(L, A). \end{aligned} \tag{9}$$

The form of the function $K_o$ is given in the next section (equation 16).

Implementing the model now requires us to specify functional forms for the

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equations relating assimilation (or ingestion) to length, maintenance to weight, and the default partitioning function $K_o(L, A)$ to length and assimilation rate. This is the subject of the next section. However, it is important to realize that the energy-channelling scheme of the above section does not rely on these particular forms. Thus when testing the model against experimental information it is important to distinguish *a priori* whether we are testing the fundamental partitioning rules, or the effects of any particular functional form or parameter selection.

## *(B) The model functions and parameters*

### *Length and weight*

The model as formulated in the previous section requires a relationship between length and weight (in carbon units) for a daphnid stripped of eggs immediately after the moult. The literature contains an apparently wide range of observed relationships between length and carbon content or dry weight, but careful examination of these results for one species (*D. pulex*) shows that most of the data are consistent with the interpretation that there is a single allometric relationship between carbon content and carapace length, valid for both adults and juveniles, which is, at most, weakly dependent on the food regime in which the animals were living. This is given in equation (1) above.

### *Ingestion and assimilation*

For daphnids of a specified length, the dependence of feeding rate (I) on food density (F) can adequately be described by a (type 2) hyperbolic functional response; thus ingestion rate can be written in the form

$$I = I_{max}F/(F + F_h). \tag{10}$$

Our review of existing data (McCauley *et al.*, 1989b; Gurney *et al.*, 1989) suggests that we may safely assume that the half-saturation constant $(F_h)$ does not vary with length.

McCauley *et al.* (1989b) discussed the variation with length in the maximum ingestion rate $(I_{max})$, which is well fitted by the function

$$I_{max} = SL^{Q}\{1 - \exp(-(L/L_u)^{i})\}. \tag{11}$$

We follow Lampert (1975) and regard food as *assimilated* if it passes across the wall of the gut, the assimilation efficiency then being defined as the ratio of instantaneous assimilation rate to ingestion rate. Measurements of this quantity exhibit high variability, but it is not established whether the variation is systematically related to either food concentration or the size of the individual. Consequently, for our model we assume a constant assimilation efficiency, assimilation rate A then being given by

$$A = \varepsilon_A I. \tag{12}$$

### *Maintenance*

This is possibly the most elusive quantity on which we require high quality information for the model. We argued in McCauley *et al.* (1989b) that maintenance rate could be modelled as the sum of two components, the first a term proportional to weight, the second a representation of the continuous commitment of new material to make the next carapace. We thus set

$$M = \beta W + T_m^{-1} W_s, \tag{13}$$

where $T_m$ is the intermoult duration, and $W_s$ is the weight of a cast skin which varies with body weight as

$$W_s = 0{\cdot}016\ W^{1.47} \tag{14}$$

when both quantites are measured in units of micrograms dry weight (Lynch, Weider & Lampert, 1986). It turns out that the use of equations (13) and (14) to specify maintenance makes simple analytic calculations of such quantities as maximum length or brood size unacceptably awkward. For practical convenience we therefore assume an allometric maintenance-weight relationship of the form

$$M = BW^{Y} \tag{15}$$

and calculate parameters B and Y so as to make the resulting curve as close as possible (which turns out to mean almost indistinguishable to graphical accuracy) from that implied by equations (13) and (14).

For detailed justification of these assumptions we refer the reader to McCauley *et al.* (1989b). However, it is important to note that our representation, in which total *maintenance* scales as weight to some power greater than one, is consistent with the common claim (e.g. Peters, 1983) that *respiration* in ectotherms scales as $W^{0.75}$. The reconciliation comes through work of Kooijman (1986b) who recently interpreted many observed relationships between respiration rate and weight as the sum of two terms: the true routine metabolism (assumed proportional to weight) and a term representing the overheads on growth (assumed proportional to the instantaneous assimilation rate).

*Allocation to reproduction*

Gurney *et al.* (1989) propose that the dependence of the allocation function on assimilation rate is treated by first introducing a quantity $K_u$:

$$\begin{aligned} &\text{If } L < L_m \text{ then } K_u = 1.0 \\ &\qquad\qquad\quad \text{else } K_u = (A_k + 1)/(A_k + A/A_{max}). \end{aligned} \tag{16a}$$

McCauley *et al.* (1989b) give a table, based on data in Paloheimo, Crabtree & Taylor (1982), from which we can infer the length dependence of the allocation function $K_0(L, A)$, a reasonable representation of very sparse data being obtained by fitting a clipped exponential function. Finally, $K_0$ is calculated from the rule

$$\begin{aligned} &\text{If } K_u < 1.0 \text{ then } K_0(L, A) = K_u + (1 - K_u) \exp\{(L_m - L)/L_s)\} \\ &\qquad\qquad\qquad \text{else } K_0(L, A) = 1.0 \end{aligned} \tag{16b}$$

in which the exponential term represents a gradual 'switch-on' of commitment to reproduction before and after the primiparous instar.

TABLE 2. The parameter set for the model of individual growth and reproduction for *D. pulex* at 20°C–from Gurney *et al.* (1989)

| Parameter | Value | Units | Brief description |
|---|---|---|---|
| $S$ | $9.54 \times 10^{-3}$ | $\text{mgC day}^{-1}\ \text{mm}^{-Q}$ | Constant in ingestion function |
| $Q$ | 1.76 | dimensionless | Index in ingestion function |
| $L_u$ | 0.95 | mm | Constant in ingestion function |
| $i$ | 2.14 | dimensionless | Index in ingestion function |
| $F_h$ | 0·164 | $\text{mgC l}^{-i}$ | Half saturation constant |
| $\varepsilon_A$ | 0.6 | dimensionless | Assimilation efficiency |
| $B$ | 0.28 | $(\text{mgC})^{1-Y}\text{day}^{-1}$ | Coefficient in maintenance –weight relationship |
| $Y$ | 1.14 | dimensionless | Allometric index in maintenance –weight relationship |
| $K_{min}$ | 0.18 | dimensionless | Minimum allocation to growth + maintenance |
| $A_K$ | 0.15 | dimensionless | Parameter in allocation function |
| $L_m$ | 0.9 | mm | Minimum length to allocate energy to reproduction |
| $L_s$ | 0.33 | mm | Constant in energy partitioning formula |
| $P$ | 2.4 | dimensionless | Allometric index for weight-length conversion |
| $W_{e\infty}$ | $0.4 \times 10^{-3}$ | $\text{mgC egg}^{-1}$ | Minimum weight of an egg |
| $W_{e\alpha}$ | $1{\cdot}4 \times 10^{-3}$ | $\text{mgC egg}^{-1}$ | Constant in formula determining egg weight |
| $L_n$ | 0.6 | mm | Length of a neonate |
| $T_m$ | 2 | day | Average instar duration |

*The model parameters*

We have derived one complete set of parameters for the model—for *D. pulex* at 20°C. These are presented in Table 2. Preparation of this table involved making a number of judgements additional to those required in formulating the model, for example selecting between conflicting data on ingestion and assimilation rates. We refer the reader to the appendix of Gurney *et al.* (1989) for further details.

### *(C) Testing the model*

*Qualitative predictions on starvation and recovery*

From the start of this paper we have recognized that the ability to model life at low food is vital; indeed the fundamental structure of the model, and much of its complexity, is the result of attention to detail in this regard. Thus before proceeding to quantitative tests of the model, it is appropriate to look qualitatively at its predictions regarding starvation and recovery.

If an animal is assumed to be capable of surviving a bout of starvation until its weight drops to a specified fraction (f) of its weight-for-length, then it is straightforward to derive an approximation to the starvation time ($T_s$) of an individual, namely

$$T_s = \log_e f/(\text{fractional daily maintenance rate at start of starvation}). \quad (17)$$

Since we relied heavily on qualitative information from starvation experiments in formulating the model, and used data on weight loss during starvation as part of our calculation of the maintenance parameters, prediction of starvation times for *D. pulex* is not a valid test of the model. However, the model also makes predictions about recovery from starvation, which ought to be amenable to experimental test. Suppose an adult has starved for a few days and has a weight less than its weight for length. If it is now introduced to food of constant density, our energy allocation rules imply that it allocates all assimilate to growth and maintenance until it regains its weight-for-length. It can be shown (after some algebraic manipulation) that there are now three possibilities.

(i) If the food density is sufficiently high, the weight-for-length is eventually achieved and commitment to reproduction resumes.

(ii) At sufficiently low food density, weight continues to decline until it reaches the value f times the weight-for-length, whereupon the animal dies of starvation.

(iii) For an intermediate range of food levels, the weight grows or declines to an asymptotic level where the animal neither dies of starvation nor resumes reproduction.

We know of no existing data against which these predictions may be tested, but have in progress a series of experiments on starvation/recovery designed to test them.

### *Quantitative predictions on growth and reproduction*

The effort involved in constructing a model as elaborate as this is only justifiable if it results in quantitative predictions on growth and reproduction, the latter in particular being vital for a population model. In Gurney *et al.* (1989) we reported a series of tests of the model against data from four different investigators (detailed in Table 3), using different clones of *D. pulex* and different experimental procedures. All but one of the sets of experiments (Taylor, 1985) used a *transfer culture* technique in which animals were grown in individual containers and transferred at regular intervals to new containers with fresh food. We selected four quantities to characterize the growth and reproduction of individuals at each food density: the maximum observed length, maximum brood size, length at first instar containing eggs, and time to first placing of eggs in the brood pouch. In Fig. 2 we show a comparison of predicted and observed values of these quantities; all except length at first brood (a quantity in which there is no obvious pattern to the original data) are well predicted by the model.

TABLE 3. Data sets used to test the model of *Daphnia* growth and development. From Gurney *et al.* (1989): A = *Chlamydomonas reinhardii*; B = *Scenedesmus acutus*

| Worker(s) | Number of individuals per container | Food type | Food conclusion (mgC $l^{-1}$) | Value (ml) | Renewal |
|---|---|---|---|---|---|
| Richman (1958) | 1 | A | 0.58 | 10 | Daily transfers |
| | 1 | A | 1.15 | 10 | Daily transfers |
| | 1 | A | 1.73 | 10 | Daily transfers |
| | 1 | A | 2.30 | 10 | Daily transfers |
| Paloheimo *et al.*, (1982) | 1 | A | 4.2 | 100 | Daily transfers |
| Taylor (1985) | 5–15 | B | 0.1 | 200 | Dilution (7.5 $d^{-1}$) |
| Taylor & Gabriel (1985) | 5–15 | B | 0.2 | 200 | Dilution (7.5 $d^{-1}$) |
| | 5–15 | B | 1.0 | 200 | Dilution (7.5 $d^{-1}$) |
| Lynch *et al.*, (1986) | 1 | A+B | 1.54 | 40 | Two-day transfers |

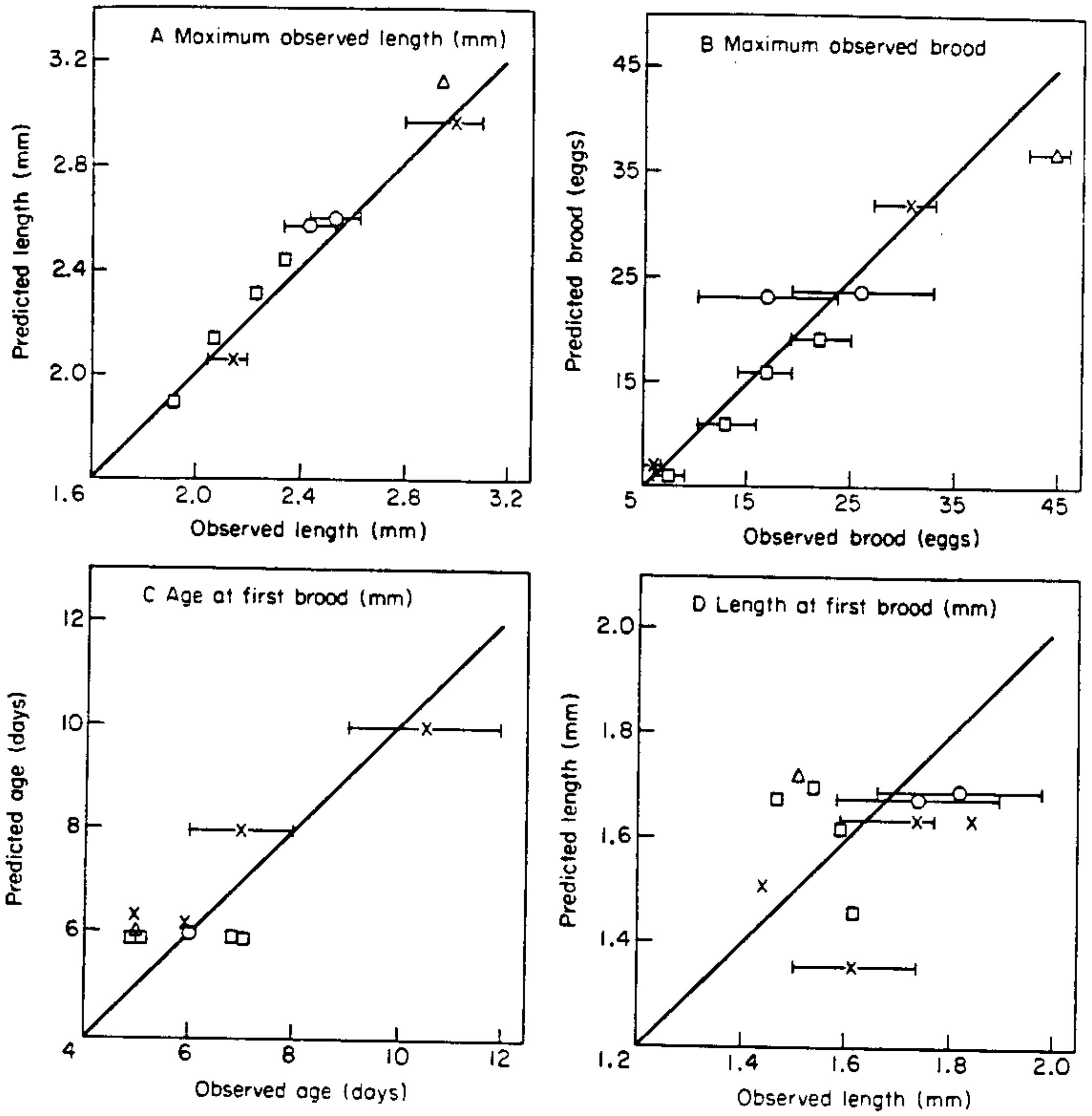

Figure 2. Predicted and observed life-history characterizations for the model of individual growth and reproduction of *D. pulex*. The sources of data (detailed in Table 3) are: Paloheimo *et al.*, 1982 (□), Lynch *et al.*, 1986 (○), Richman, 1958 (△), and Taylor, 1985 (×). Figure reproduced from Gurney *et al.* (1989).

This success is an encouraging start to the wider programme of relating individual and population phenomena; at least it is possible to construct a model in which parameters derived largely from short-term measurements of physiological rate processes are used to successfully predict individual growth and reproduction.

## A STAGE-STRUCTURED POPULATION MODEL

### *(A) Model formulation*

Having constructed a model of individuals we might now expect to be able to use techniques similar to those in Metz & Diekmann (1986: chapter 3) to construct a population model. Their approach, which to the best of our understanding reflects the current mathematical state of the art, involves selecting a set of variables which specify the *state* of an individual (i-state); the individual model then gives us the differential equations which describe the change with time of these state variables. The population dynamics are given by partial differential equations or integral equations which are numerically tractable only if the equations in the individual model are reasonably well behaved. Unfortunately, certain key variables in our individual model change discontinuously (at moults), while derivatives of all the state variables may change discontinuously, for example when food drops so that an animal enters starvation. We are therefore some way away from being able to follow this approach to a population model.

The same discontinuities cause difficulty if we adopt a 'brute force' approach and, arguing that a population is simply a collection of individuals, model a small volume containing (say) tens of individuals by solving numerically the differential equations for each individual. There are now many non-analytic points in the solutions, and it is our experience that these have to be located rather accurately to avoid large numerical error. These problems are superable (but only with considerable effort) and we are pursuing this approach further.

Faced with these difficulties, we have temporarily compromised our original objective of deriving a structured model based strictly on the individual model, and formulated a stage-structured 'continuous development' model in which the life history is subdivided into a number of physiological stages, within which development and mortality rates vary continuously and are assumed to have the same values at any given time. The methodology has been described in detail elsewhere (Gurney, Nisbet & Lawson, 1983; Nisbet & Gurney, 1983; Gurney, Nisbet & Blythe, 1986), here we merely note that the pay-off from this simplification is that the population dynamics may be described in terms of a relatively small number of delay-differential equations whose numerical solution is fairly straightforward.

In our stage-structured model, we recognize three stages—juveniles (whose density is denoted by J), young adults (density Y), and mature adults (density A)—all of which are assumed to eat a common food of (carbon) density F. *Juveniles* are defined to be individuals which commit, or have the capacity to commit, all excess assimilate not required for maintenance, to growth. The *young adult* stage covers the period (roughly two moults) that elapses between the first commitment (or capacity for commitment) of assimilate to egg production and the release of the first brood of neonates. The *adult* stage covers the entire remainder of the animal's life. The densities for the three stages then must satisfy the following balance equations

$$dJ(t)/dt = R_J(t) - M_J(t) - m_J(t)J(t) \tag{18}$$

$$dY(t)/dt = R_Y(t) - M_Y(t) - m_A(t)Y(t) \tag{19}$$

$$dA(t)/dt = R_A(t) - m_A(t)A(t) \tag{20}$$

which are coupled through the various vital rate functions to an equation describing the balance of supply and consumption of food namely

$$dF(t)/dt = R_F(t) - J(t)I_J(t) - [Y(t) + A(t)]I_A(t). \tag{21}$$

In these equations, at time t: $R_F(t)$ = food replacement rate per unit volume;

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$I_J(t)$ = feeding rate (mgC per day) for juveniles; $I_A(t)$ = feeding rate (mgC per day) for adults; $R_J(t)$ = recruitment rate per unit volume of juveniles; $R_Y(t)$ = recruitment rate per unit volume of young adults; $R_A(t)$ = recruitment rate per unit volume of adults; $M_J(t)$ = maturation rate per unit volume of juveniles; $M_Y(t)$ = maturation rate per unit volume of young adults; $m_J(t)$ = per capita death rate of juveniles; $m_A(t)$ = per capita death rate of adults.

For each stage we are required to define a *development index* (or physiological age) such that individuals mature to the next stage when their development index attains a particular value. This permits us to relate the rate of maturation out of a stage to the rate of recruitment to the stage at some previous time. The remaining steps in the formulation of the model involve assumptions on mortality within and between stages, and assumptions on fecundity. A full account of the basis for these assumptions and of the details of parameter estimation will be published elsewhere; however as with the individual model, following the programme through involves making a significant number of biological judgements and using our own data to fill gaps in the literature. These aspects we highlight in the next two subsections (B and C), and some preliminary tests of the model are presented in subsection D. The full set of equations defining the model is given in Table 4 and a provisional set of parameter values in Table 5.

TABLE 4. Formulae for the 'continuous development' *Daphnia* population model

| | |
|---|---|
| Food and feeding: | $F(t) = R_F(t) - J(t)I_J(t) - [Y(t) + A(t)]I_A(t)$<br>$I_J = \frac{I_{mJ}F}{F + F_h} \quad I_A = \frac{I_{mA}F}{F + F_h}$<br>$\bar{I}_J(t) = T_m^{-1} \int_{t-T_m}^{t} I_J(x)\,dx \quad \bar{I}_A(t) = T_m^{-1} \int_{t-T_m}^{t} I_A(x)\,dx$ |
| Juvenile development: | $h_J(t) = T_{max}^{-1} + [T_{min}^{-1} - T_{max}^{-1}] \frac{[\varepsilon_{AJ} I_J(t) - \Gamma_J]_+}{[\varepsilon_{AJ} I_{mJ} - \Gamma_J]}$ |
| Fecundity: | $\beta(t) = e[\varepsilon_{AA} \bar{I}_A(t - T_m) - \Gamma_A]_+$ |
| Mortality: | $m_J(t) = m_{oJ} + m_{aJ} \exp[-\bar{I}_J(t)/I_{JO}]$<br>$m_A(t) = m_{oA} + m_{aA} \exp[-\bar{I}_A(t)/\bar{I}_{AO}]$ |
| Juvenile development times: | $\dot{\tau}_J(t) = 1 - h_J(t)/h_J(t - \tau_J(t))$ |
| Through-stage survival: | $\dot{P}_J(t) = P_J(t)\left[m_J(t - \tau_J(t)) \frac{h_J(t)}{h_J(t - \tau_J(t))} - m_J(t)\right]$<br>$\dot{P}_Y(t) = P_Y(t)[m_A(t - 2T_m) - m_A(t)]$<br>$S_{JY}(t) = 1 - \exp[-(T_{max} - T_J(t)/T_o)]$ |
| Recruitment and maturation: | $R_J(t) = \beta(t)A(t)$<br>$M_J(t) = R_J(t - \tau_J(t))P_J(t) \frac{h_J(t)}{h_J(t - \tau_J(t))}$<br>$R_Y(t) = M_J(t)S_{JY}(t)$<br>$M_Y(t) = R_Y(t - 2T_m)P_Y(t)$<br>$R_A(t) = M_Y(t)$ |
| Population balance equations | $\dot{J}(t) = R_J(t) - M_J(t) - m_J(t)J(t)$<br>$\dot{Y}(t) = R_Y(t) - M_Y(t) - m_A(t)Y(t)$<br>$\dot{A}(t) = R_A(t) - m_A(t)A(t)$ |

TABLE 5. A provisional parameter set for the 'continuous development' population model—appropriate to *D. pulex* at 20°3

| Parameter | Value | Units | Brief description |
|---|---|---|---|
| $T_{max}$ | 20 | day | Maximum development time: juveniles |
| $T_{min}$ | 4 | day | Minimum development time: juveniles |
| $T_o$ | 3.5 | day | Constant in formula for surviving maturation |
| $e$ | 1000 | $(mgC)^{-1}$ | Conversion efficiency—food to neonates |
| $F_h$ | 0.164 | mgC $l^{-1}$ | Half saturation constant |
| $I_{mj}$ | $6.5 \times 10^{-3}$ | mgC $day^{-1}$ | Maximum feeding rate: juveniles |
| $I_{ma}$ | $2.1 \times 10^{-2}$ | mgC $day^{-1}$ | Maximum feeding rate: adults |
| $\Gamma_j$ | $3.2 \times 10^{-4}$ | mgC $day^{-1}$ | Maintenance rate: juveniles |
| $\Gamma_A$ | $1.1 \times 10^{-3}$ | mgC $day^{-1}$ | Maintenance rate: adults |
| $\varepsilon_{Aj}$ | 0.6 | dimensionless | Assimilation efficiency: juveniles |
| $\varepsilon_{Aa}$ | 0.6 | dimensionless | Assimilation efficiency: adults |
| $T_m$ | 3.0 | day | Average instar duration |
| $I_{oj}$ | $4 \times 10^{-4}$ | mgC $day^{-1}$ | Constant in formula for juvenile mortality |
| $I_{oa}$ | $2 \times 10^{-3}$ | mgC $day^{-1}$ | Constant in formula for adult mortality |
| $m_{oj}$ | $3 \times 10^{-3}$ | $day^{-1}$ | Background juvenile mortality |
| $m_{oa}$ | $3 \times 10^{-3}$ | $day^{-1}$ | Background adult mortality |
| $m_{sj}$ | 0.217 | $day^{-1}$ | Maximum mortality increment: juveniles |
| $m_{sa}$ | 0.217 | $day^{-1}$ | Maximum mortality increment: adults |

### *(B) Development and maturation of juvenile daphnids*

The primary role of the juvenile development index in the population model is to determine the timing of the onset of maturation of the young adult stage. From Fig. 2D and from our own experiments, it is clear that over a wide range of food densities, the first brood appears at a certain critical length. However, our own experiments (McCauley, Murdoch and Nisbet, 1989b) point in addition to the existence of an upper duration to the juvenile stage; *D. pulex* grown at very low food densities at 20°C which survive to an age of around 20 days will attempt to produce an egg, sometimes dying as a result. Taken together, these observations point to a development index, q, which is a weighted average of age and weight. If we chose to make the development index dimensionless and specify that neonates have $q = 0$, and that maturation occurs at $q = 1$, and further accept a technical constraint that an individual's development index must never decrease as she grows older, then this suggests a development rate of the form

$$h(t) = dq/dt = T_{max}^{-1} + \frac{T_{min}^{-1} - T_{max}^{-1}}{[\varepsilon_{Aj} I_{mj} - \Gamma_j]} [\varepsilon_{Aj} I_j(t) - \Gamma_j]_+ \qquad (22)$$

where $T_{max}$ and $T_{min}$ are respectively the minimum and maximum development times for a juvenile, $\varepsilon_{Aj}$ represents the assimilation efficiency of a juvenile, $\Gamma_j$ its maintenance requirements (mgC $day^{-1}$), and $I_{mj}$ its maximum possible feeding rate. The notation $[\ ]_+$ is a shorthand form for the rule that if the value of the quantity in square brackets is negative, it is replaced by zero when evaluating the formula.

Figure 3 shows that, with this choice of development index, there is a satisfactory fit to both our own measurements of juvenile stage duration and to the data used by Gurney *et al.* (1989) and reproduced in Fig. 2 in the tests of our individual model.

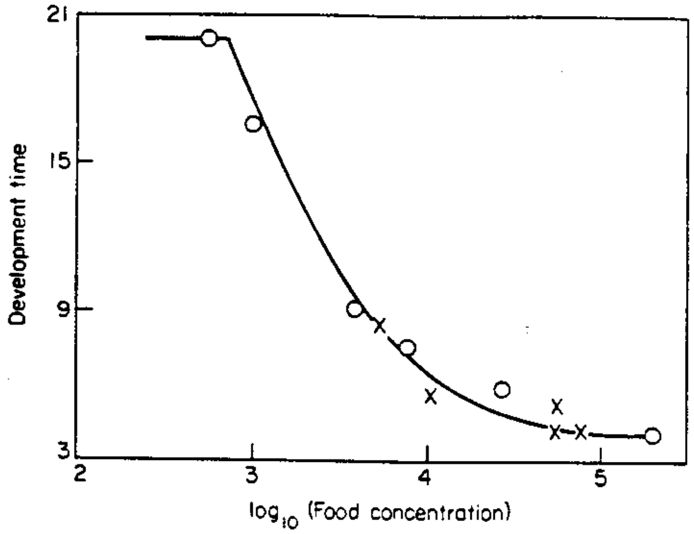

Figure 3. Juvenile development time versus food concentration for *D. pulex* at 20°C. Data from McCauley *et al.*, 1989a (○), Fig. 2 (×).

### *(C) Assimilation of food, mortality and reproduction*

The current 'continuous development' model deliberately neglects the discrete nature of daphnid development, largely on the grounds of technical expediency. Yet our tests of the individual model demonstrated the importance of this aspect, and we require some 'fix' to ensure that we capture the way in which the production of discrete broods smooths out the effect of large, short-term fluctuations in food supply. Similar considerations arise in modelling any mortality due to starvation.

We thus choose to model both reproduction and starvation mortality via an *average* ingestion rate over a time interval equal in duration to one moult, and define

$$\bar{I}_J(t) = T_m^{-1} \int_{t-T_m}^{t} I_J(x)\,dx \qquad \bar{I}_A(t) = T_m^{-1} \int_{t-T_m}^{t} I_A(x)\,dx. \tag{23}$$

To model fecundity, we recognize that neonates released at time t have developed from eggs transferred to the brood pouch at time $t-T_m$. It thus seems appropriate to assume that fecundity depends on $\bar{I}_A(t-T_m)$; indeed we assume that a fixed fraction of all excess assimilate over and above that needed for maintenance goes to reproduction, implying that the instantaneous fecundity is given by

$$\beta(t) = e[\varepsilon_{Aa}\bar{I}_A(t-T_m) - \Gamma_a]. \tag{24}$$

Far less information is available about mortality rates for individual daphnids than is available on growth and reproduction. In particular, we know of no published life tables at different food levels for *D. pulex*, the species we chose to test our model of growth and reproduction. Our representation of mortality thus rests on an interpretation of data for other species (*D. galeata*: Goulden, Henry & Tessier, 1982; *D. magna*: Porter, Orcutt & Gerritsen, 1983), and on preliminary analysis of our own (unpublished) experiments.

We have identified four components of mortality in laboratory populations.
(1) Background.
(2) Senescence.
(3) Starvation.
(4) Production of first brood.

*Background* mortality is generally agreed to be low. *Senescence* is well documented, there being good evidence (Porter *et al.*, 1983) that life is shorter when food is plentiful. We are currently evaluating evidence that might give pointers to the mechanisms of senescence in *Daphnia*; pending completion of this investigation we have not incorporated senescence explicitly in the model, but instead modify the assumed background mortality rate to give plausible average lifetimes.

To model *starvation mortality*, we again argue that the appropriate determinant is likely to be average food intake over a time comparable with one moult, and on the grounds of parsimony assume dependence on the same averages (equation 23) already used in the model. It is clear from the experiments already cited that starvation mortality is only significant at very low food levels, and this leads us to assume an exponential dependence of the form

$$m_J(t) = m_{oj} + m_{sj} \exp\left[-\bar{I}_J(t)/I_{JO}\right] \tag{25}$$

$$m_A(t) = m_{oa} + m_{sa} \exp\left[-\bar{I}_A(t)/I_{AO}\right] \tag{26}$$

Finally we have included in the model a crude representation of mortality at maturation, based on our own experiments on individual *D. pulex* growing on *Chlamydomonas reinhardii* at densities of 500 cell ml$^{-1}$. We assumed that any juvenile which has not matured by age $T_{max}$ dies with 100% probability, and that any which mature at age a ( $< T_{max}$) have a probability

$$S_{JY}(t) = 1 - \exp\left[-(T_{max} - a)/T_o\right] \tag{27}$$

of surviving the transition to the immature adult stage.

### (D) *Qualitative tests of the model*

*Laboratory populations*

McCauley and Murdoch (1987: see their table 3) reviewed the available literature on laboratory population dynamics and noted that at temperatures around 18–20°C, the expected pattern of behaviour was either damped oscillations (Frank, 1960 for *D. pulex*), or low amplitude cycles (Slobodkin & Richman, 1956 for *D. pulicaria*; Marshall, 1978 and Goulden *et al.*, 1982 for *D. galeata*). The period of the persisting or damped cycles was in the range 20–40 days.

A detailed simulation of any one of these populations requires careful representation of the food replacement schedule, and determination of model parameters appropriate to the species under investigation. However, we might expect to capture the essential features, in particular the period, of the cycles with runs of the continuous development model using our *D. pulex* parameter set and a 'pseudo-chemostat' food replacement schedule in which

$$R_F(t) = D(F_r - F). \tag{28}$$

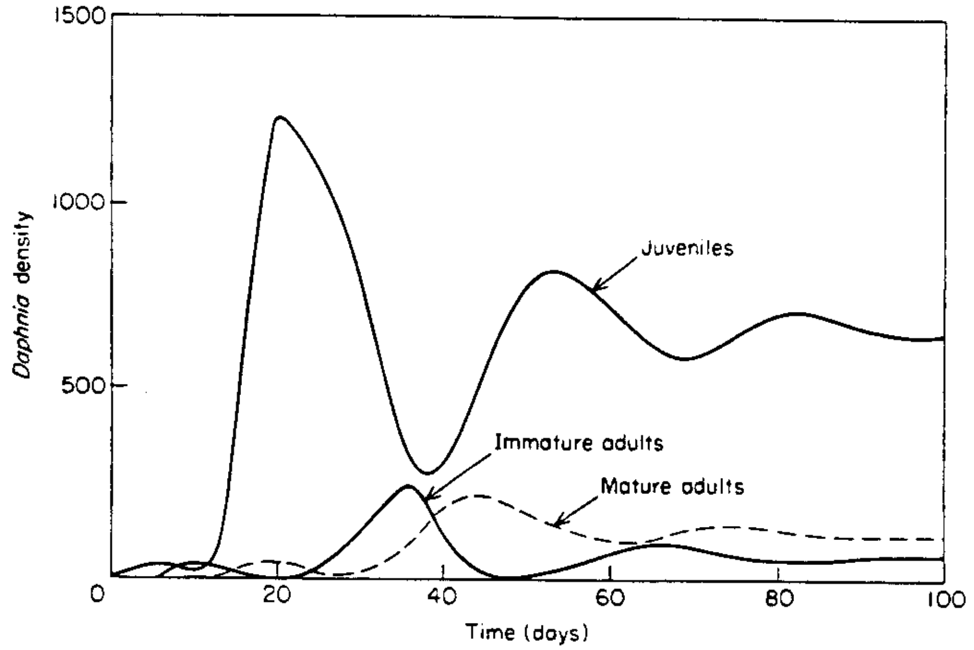

Figure 4. Predicted population dynamics for a 'laboratory' population of *D. pulex*. Details in text.

One such set of results, for a dilution rate of 1 $\text{day}^{-1}$ and a reservoir concentration of 1.0 $\text{mgC l}^{-1}$ (corresponding to $5 \times 10^4$ cells $\text{ml}^{-1}$ *Chlamydomonas reinhardii*), is shown in Fig. 4. The cycles are lightly damped, have a period in the desired range, and the demography implied by the stage populations is broadly consistent with observations. However, the detailed form of the cycles is not strictly consistent with the dominance-suppression hypothesis in the Introduction to this paper (A. de Roos, personal communication), an aspect on which we shall report in a future publication.

*Field populations*

McCauley & Murdoch (1987: see their table 2) also surveyed a number of field populations, and found examples of both 'stable' behaviour and apparent 'prey-predator' cycles, with small amplitudes (ratio of maximum to minimum populations less than four) and essentially the same range of periods as occurred in the laboratory. In examples of prey-predator cycles for which there was information on the size structure of the population, the demography was remarkably similar to that occurring in the laboratory populations.

The difficulties in a realistic simulation of field populations are even greater than those for their laboratory counterparts; the structure of the food assemblage must be considered, and *all* parameters have the potential to vary in response to changing temperature. However, it is again appropriate to investigate the qualitative predictions of our model when we introduce the one key feature that distinguishes the laboratory and field populations: self-reproducing food. We have therefore studied the behaviour of our model with a logistic food replacement function,

$$R_F(t) = rF(1-F/K). \qquad (29)$$

A typical set of results is shown in Fig. 5A and is totally inconsistent with what

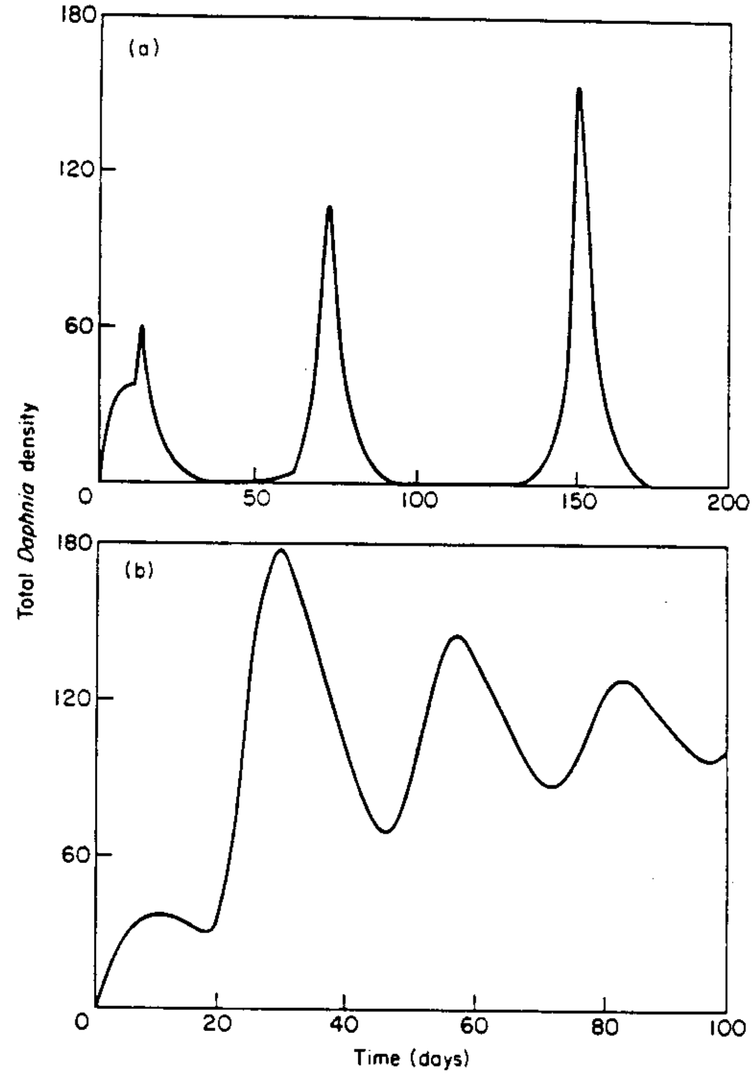

Figure 5. Predicted population dynamics for a *Daphnia* population with reproducing prey as detailed in text: A, using parameters from Table 5, and B, with $F_h$ increased by a factor of 10.

happens in the real world. The ratio of maximum to minimum populations is very large, and the minima are sufficiently small to imply extinction in practice. In addition, the period is far too long. These large amplitude limit cycles are reminiscent of those found in simple, unstructured prey-predator models as a result of the ***paradox of enrichment***, in which the combined effect of a saturating functional response for the predator and self-limitation of the prey can be to produce cycles whose very large amplitudes would in practice imply extinction (Gilpin, 1972).

We can look to this literature for guidance on which of our model assumptions and/or parameters is likely to be responsible for the unrealistic cycles. One possibility is that there is some small portion of the food inaccessible to the *Daphnia* at any given time. Such a refuge might arise if *Daphnia* avoids the top 1–2 m of lake water because of high light levels and hence high visibility to potential predators (Gulati, 1978), or on a horizontal scale in stratified systems because of Langmuir circulations (George & Edwards, 1973). We therefore performed some simulations with ***constant number refuges***. Even a refuge as low as

5% of carrying capacity is sufficient to dampen out the large amplitude prey-predator cycles, interestingly leaving behind 'single-generation cycles' with a period of the same order as that observed.

A second, and perhaps more plausible, mechanism is suggested by work of McCauley *et al.* (1988) on factors determining the equilibria of natural *Daphnia* populations. There, it was argued that the model parameters were likely to be strongly influenced by the structure of the phytoplankton assemblage, and in particular by variations in the edible fraction of the algal population. It was further argued (by reference to the daphnid's mode of eating) that the introduction of inedible food would not influence the handling time per unit of edible food, but would reduce the effective filtering rate. In terms of the parameters in Table 4, this would imply that the half-saturation constant $F_h$ is too low. We therefore performed a set of runs in which the value of this parameter was varied, one result being reproduced as Fig. 5B. Again we see the disappearance of the large-amplitude, long-period cycles and the occurrence of low-amplitude, single-generation cycles.

## DISCUSSION

The work outlined in this paper has drawn attention to the large number of biological judgements that are necessary when constructing an individual model, even for a genus as well studied as *Daphnia*. We arrived at an individual model that is inelegant and parameter-rich, but is consistent with a rather wide body of experimental data. Clearly an important component of future work should be a search for simpler individual models which retain the capacity to predict growth and fecundity over a wide range of food densities and in rapidly varying conditions.

Further study is also needed on some technical problems associated with the transition from individual to population models. Our 'continuous development' population model does appear to be a useful simplification, but we would feel safer using it if we knew how its properties compare with those of a model rigorously derived from our individual model.

However, the central, still unanswered question is this: can structured population models help us understand the factors responsible for determining population sizes and patterns of fluctuations in natural populations? The approach to population modelling adopted in this paper is deliberately unbalanced: we work from a detailed account of the individual behaviour of members of the population under investigation, yet include as little detail as possible on the environmental factors (such as 'food') that drive the population dynamics. We do this, fully recognizing that real, natural populations are spatially heterogeneous, and form part of a multi-species community in which the dynamics of each species is potentially influenced by many others. The broad justification is that this approach opens the possibility of quantifying the relative importance of the many factors that *may* influence the population dynamics. A lake may not be merely a 'scaled-up' litre flask, but the analyses of McCauley & Murdoch (1987) suggest that *Daphnia* populations may behave similarly in both systems; structured models can sharpen our understanding of the ways in which they differ, thereby contributing significantly to our understanding of natural populations.

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