Ecological Monographs, 66(4), 1996, pp. 479–501

STRUCTURED POPULATION MODELS OF HERBIVOROUS ZOOPLANKTON[1]

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Abstract. In this paper, we investigate whether a stage-structured population model can explain major features of dynamics of the herbivores *Daphnia galeata* and *Bosmina longirostris* reared under controlled laboratory conditions. Model parameters are determined from independent individual-based information gleaned from the literature on feeding, growth, reproduction, and survivorship of these herbivores. We tested predictions of our model against published observations on the dynamics of laboratory populations. The feeding protocols used in these experiments present a highly dynamic food environment that rigorously challenges the ability of stage-structured models to predict the dynamics of populations as they approach equilibrium. For both herbivore species, the models correctly predict feasible equilibria and some features of their dynamics (e.g., periodicity, cycle amplitude, demography, and fecundity) for experiments in which the species were raised in isolation and food transfers were relatively frequent (at least one transfer per instar). With frequent food transfers, the model also correctly predicts coexistence of the herbivores during competition experiments and suggests a novel mechanism for coexistence. The model fails to predict correctly single-species dynamics and the outcome of competition in experiments where food transfers were infrequent and utilization of internal reserves by individuals in the populations must have been high.

Key words: Bosmina; Daphnia; *modelling dynamics of competitors; population dynamics; stage-structured population models.*

INTRODUCTION

Herbivorous zooplankton, such as *Daphnia*, and their algal prey display a range of population dynamics in lakes and ponds (e.g., Murdoch and McCauley 1985, McCauley and Murdoch 1987, Borgmann et al. 1988, Lampert 1988, McCauley et al. 1988). For situations where *Daphnia*'s predators are unimportant, there is compelling evidence for the hypothesis (McCauley and Murdoch 1987, 1990) that these dynamics are internally generated by the predator–prey interaction between herbivores and their algal prey, as opposed to being externally driven by environmental variability during the growing season (McCauley 1993). Explanations for the observed range of dynamics, and, in particular, mechanisms producing cycles have thus focused on the interaction between individual herbivores and their food supply (e.g., McCauley and Murdoch 1987, 1990, Borgmann et al. 1988, McCauley et al. 1988, Nisbet et al. 1989, Arditi et al. 1991, Kretzchmar et al. 1993, Grover 1995; W. W. Murdoch, R. M. Nisbet, E. McCauley, A. M. de Roos, and W. S. C. Gurney, *unpublished manuscript*).

Fortunately, there is a tremendous amount of qualitative and quantitative information on energy acquisition and utilization by herbivorous zooplankton (e.g., Richman 1958, Lampert 1977, Paloheimo et al. 1982, Porter et al. 1982, Taylor 1985, Lynch et al. 1986, McCauley et al. 1990*a*, *b*; Glazier 1992). The availability of these data provides a unique opportunity to examine whether individual-based models of the predator–prey interaction can explain population level dy-

[1] Manuscript received 26 June 1995; revised 8 January 1996; accepted 8 January 1996.

namics and provide insight as to how the range of dynamic behavior observed in natural systems is produced.

In this paper, we focus on whether a structured population model for herbivorous zooplankton, developed using independent physiological data, can predict population dynamics under laboratory conditions. Laboratory-raised populations are often viewed as being artificial systems, which are unlikely to provide any insight on the dynamics of "real" populations in natural environments. However, there are several reasons why tests against laboratory populations are illuminating in this case. First, we have demonstrated previously (McCauley and Murdoch 1987, 1990) that cycles in field and laboratory populations share many demographic features, including fluctuations in age structure and fecundity. Second, the feeding protocol in many laboratory experiments, which typically consists of batch addition of food at discrete intervals (e.g., Slobodkin 1954, Goulden et al. 1982), provides one of the most stringent tests of a model's ability to capture the dynamics of herbivore energetics. In general, we often imagine laboratory culture conditions as being relatively benign with respect to environmental variation compared with "natural" systems, and while these laboratory experiments certainly hold constant many aspects of the physical environment (e.g., temperature, photoperiod, etc.), the food is highly dynamic over the time scale of the transfer interval. Individuals in these laboratory populations experience a rapidly fluctuating food environment on the time scale of their molt cycle (during which energy is being allocated dynamically to competing processes of growth, reproduction, and mortality), and this provides a rigorous challenge for the model to integrate accurately the interaction between individuals and their food environment.

We have previously developed (Nisbet et al. 1989) a structured population model for *Daphnia pulex* based on a synthesis of individual physiology (Gurney et al. 1990, McCauley et al. 1990*a*, *b*). Here we examine whether this model can be applied to another *Daphnia* species (*D. galeata*) for which there are excellent data on laboratory population dynamics. We then examine whether this model can predict the dynamics of a freshwater herbivore from a different genus (*Bosmina longirostris*) that has some contrasting life history features. To estimate the required parameters on feeding, development, reproduction, and survivorship for *D. galeata* and *B. longirostris*, we synthesized quantitative data from the literature on the physiological ecology of these species. Finally, we examine whether our model can predict the dynamics of competing populations of *D. galeata* and *B. longirostris*.

The development and testing of individual-based modelling approaches is in its infancy (e.g., Metz and Diekmann 1987, De Angelis and Gross 1992, Judson 1994) and, despite the immediate appeal to biologists of providing predictions that can be used to distinguish plausible explanations, there have been significant criticisms of the approach. Some believe these models will provide limited biological insight because of their inherent complexity and their lack of generality (Judson 1994). A thorough investigation of these issues is beyond the scope of this paper. However, by examining the ability of a single structured population model to capture the population dynamics of a suite of herbivore species, we hope to provide at least one example that can contribute to the debate on the role of individual-based theory in population ecology, and also to the wider issue of reconciling the conflicting demands of generality vs. testability in ecological models.

Target Data

Laboratory experiments on the population dynamics of *Daphnia* have been widely used to test fundamental ideas in population ecology, such as density-dependent regulation (e.g., Frank et al. 1957, Frank 1960) or the role of time delays (e.g., Pratt 1947; Slobodkin 1954, Goulden and Hornig 1980, Goulden et al. 1982). These experiments often use a protocol in which populations are raised in fixed volumes and transferred on a regular basis to a fresh universe containing a known amount of food. Throughout this paper we use the term "transfer culture" to describe this protocol.

Despite the fact that many of these experiments are "classics," Van der Hoeven (1989) has recently suggested that, strictly speaking, most of them suffer from "demonic intrusions" or external factors that produce perturbations in the density or age structure of the population that renders problematic the interpretation of the causes of population dynamics. The study with perhaps the best control over food supply, initial states, and experimental conditions is Goulden et al. (1982). Goulden's experiments are particularly well suited for modeling, as the carbon content of cells provided as food was measured directly (Goulden and Hornig 1980). Populations of three species of cladocerans (*Daphnia magna*, *D. galeata*, and *Bosmina longirostris*) were raised in isolation and in competition at various food levels. We consider in this paper only the dynamics of *D. galeata* and *B. longirostris*, because of inadequate data to parameterize fully a stage-structured model of *D. magna*. In this section, we summarize the essential dynamical features of the populations studied by Goulden et al. (1982). These populations were censused, so none of the observed fluctuations is attributable to sampling error. For brevity, we refer to the subspecies *D. galeata mendotae* studied by Goulden et al. (1982) as *D. galeata* (see Appendix for taxonomic considerations).

Figs. 1 and 2 show dynamics of *D. galeata* populations observed for two different food regimes: (1) a treatment labeled "medium food" by Goulden et al., in which a 50:50 mixture of *Chlamydomonas reinhardtii* and *Ankistrodesmus falcatus*, with a C concentration of 0.25 mg/L, was provided every 2 d (Fig. 1),

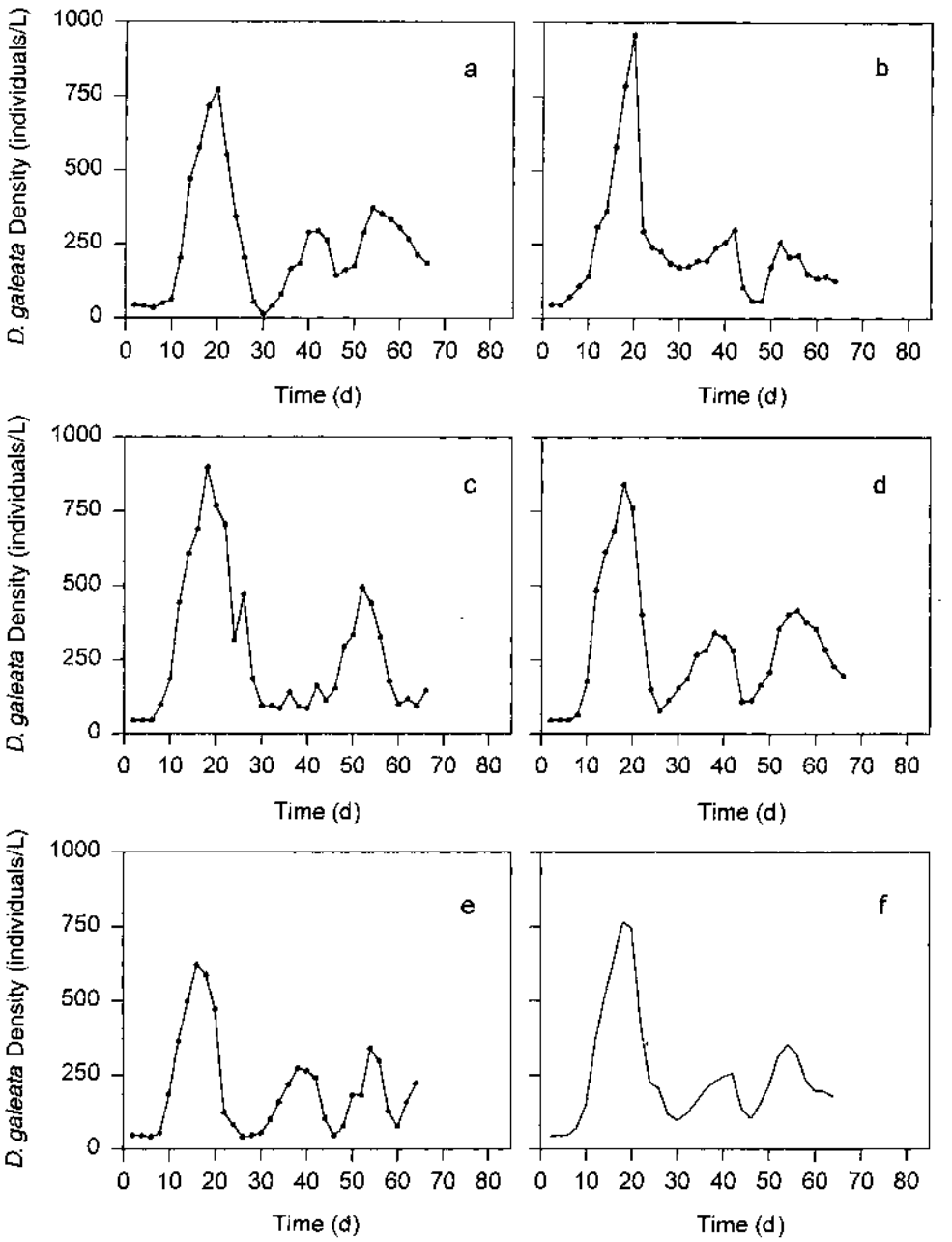

FIG. 1. Dynamics of replicate populations of *Daphnia galeata* observed by Goulden et al. (1982) when populations were provided food with 0.25 mg C every 2 d. Total density re-expressed from the original paper as number of individuals per litre. a–e, replicate populations; f, fluctuations averaged over replicates.

and (2) a "high food" treatment, with a C concentration of 2.5 mg/L, was provided every 4 d (Fig. 2). As the interval between transfers turns out to play a significant role in our interpretation of these experiments, we shall refer to the experiments as "2-d" and "4-d" transfer cultures.

In the 2-d transfer cultures (Fig. 1), all populations displayed an initial overshoot in density, peaking by roughly day 18, followed by small-amplitude fluctuations with no extinctions. Beyond these major similarities in dynamics, there was considerable variation observed among replicates after the initial overshoot, especially in the number and amplitude of the "cycles." For example, four of the replicates (Fig. 1a, b, d, e) have a second peak in density at approximately day 40. In three of these four replicates (Fig. 1 a, d, e), the third peak in density, at approximately day 55, was higher than the second peak. The second peak at day 40 seems to be much reduced in one replicate (Fig. 1c), and there is a peak that occurred just after day 50.

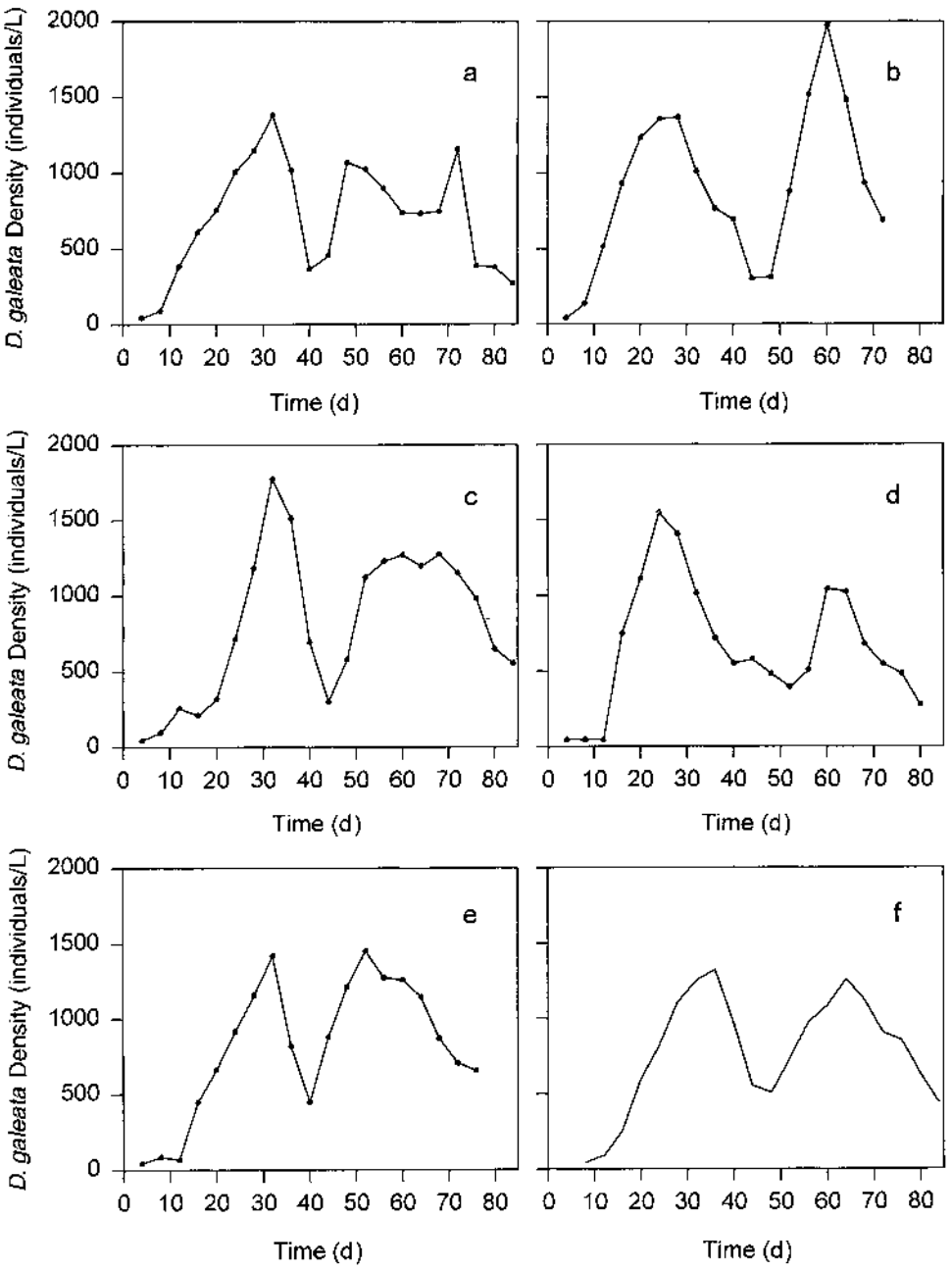

FIG. 2. Dynamics of replicate populations of *Daphnia galeata* observed by Goulden et al. (1982) when populations were provided food with 2.5 mg C every 4 d. Total density re-expressed from the original paper as number of individuals per litre. a–e, replicate populations; f, fluctuations averaged over replicates.

Goulden et al. (1982) paid strict attention to the initial experimental conditions. Each replicate was started with 10 neonates of identical age born to mothers of the same age and identical feeding history. The ensemble average of the dynamics can be determined by calculating the average density among replicates for each time period (Fig. 1f). On average, the initial large overshoot (i.e., peak of the first cycle) was followed by small-amplitude cycles, with the zenith of the second cycle smaller than the peak of the third cycle.

The demography of the populations reared in the 2-d transfer cultures is shown in Fig. 3. As described by Goulden et al., the populations tend to be dominated numerically by juveniles, typically representing >75–80% of the total population. The only estimate of fecundity is provided by observations of the proportion of ovigerous females in the population. The brood size for females carrying eggs was not recorded, and thus it is difficult to draw inferences about the degree of fluctuations in fecundity, since the number of eggs per

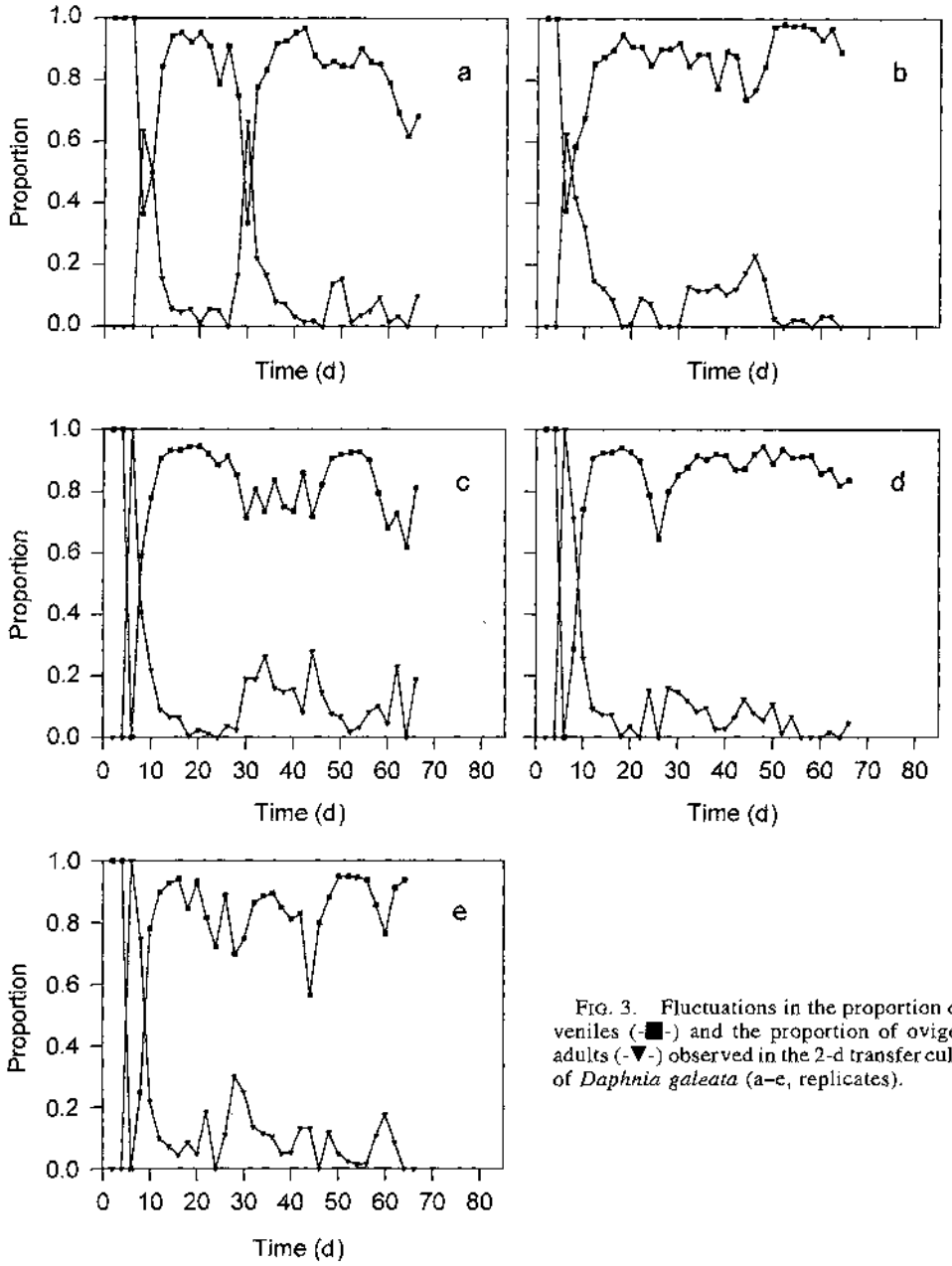

FIG. 3. Fluctuations in the proportion of juveniles (-■-) and the proportion of ovigerous adults (-▼-) observed in the 2-d transfer cultures of *Daphnia galeata* (a–e, replicates).

brood may have varied also. However, during the initial overshoot in density there is clear fecundity suppression that occurred at approximately peak density in all replicates (i.e., day 18–24), and following this period of suppression, there was a burst of reproduction (i.e., day 25–35) with subsequent fluctuations in the percentage of females with eggs occurring within a relatively narrow range (i.e., 0–25%).

While the dynamics observed in 4-d transfer cultures (Fig. 2) shared some features with the 2-d transfers, there were significant differences in the timing and amplitude of the fluctuations. The initial peak in density occurred roughly by day 30, with the subsequent nadir of the cycles occurring between day 40–50. (Please note: care must be taken in interpreting the magnitude of the differences and the exact timing of dynamical features between treatments because of the differences in sampling frequency.) All but one replicate (i.e., Fig. 2b–e) displayed a single cycle of comparatively long duration following the initial cycle, and the peak of the second cycle was generally less than the peak of the first cycle (i.e., Fig. 2a, c–e). The differences in periodicity between treatments were also noted by Van der Hoeven (1989). Fig. 2f shows the average dynamics for this treatment.

As reported by Goulden et al. (1982), the proportion

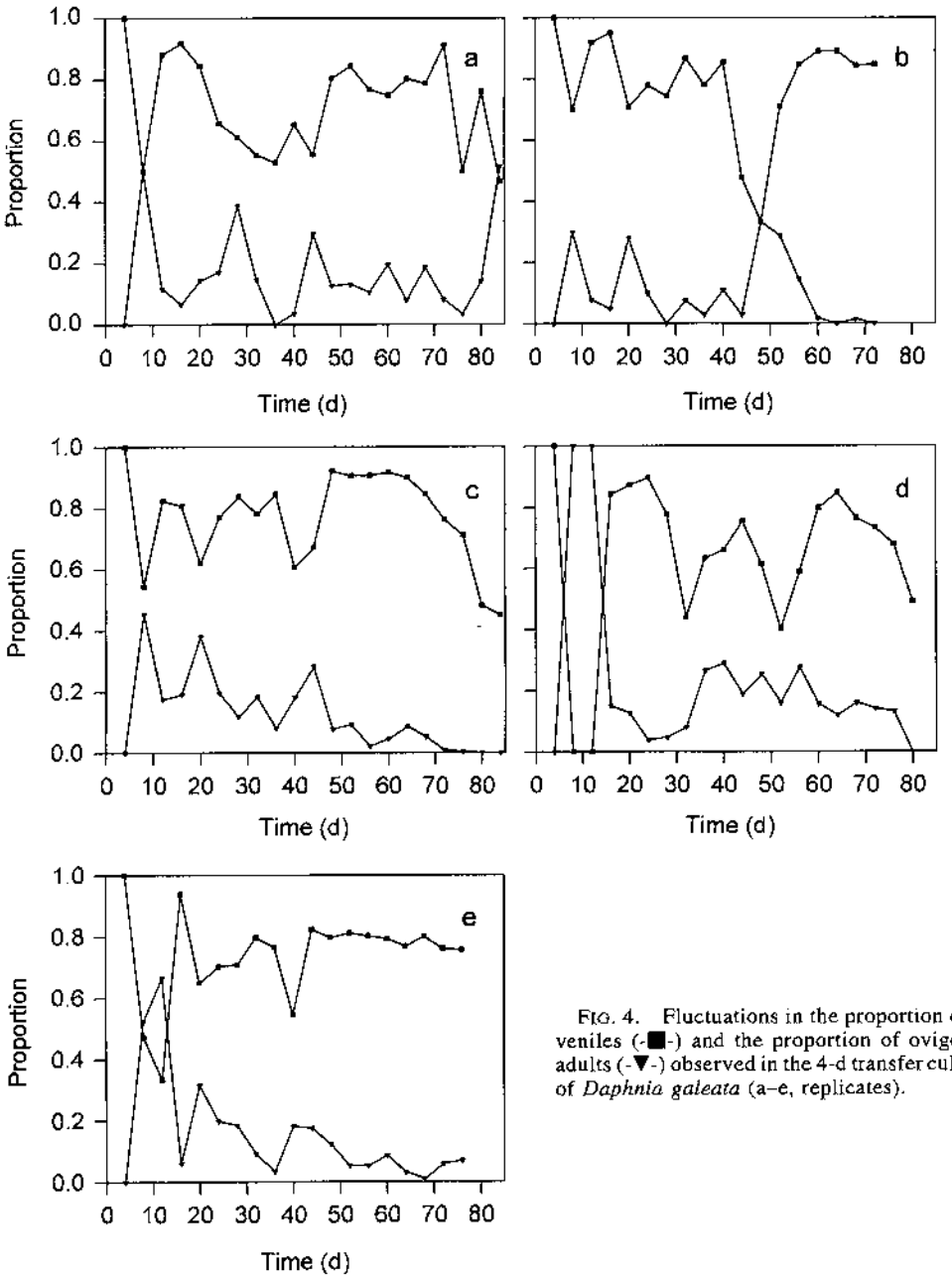

FIG. 4. Fluctuations in the proportion of juveniles (-■-) and the proportion of ovigerous adults (-▼-) observed in the 4-d transfer cultures of *Daphnia galeata* (a–e, replicates).

of adults in the 4-d transfer cultures increased (cf. Figs. 3 and 4) relative to the 2-d transfers. The level of fecundity suppression also appears to have changed between treatments (Fig. 4). In the 4-d transfer cultures, the proportion of ovigerous females was higher on average, and bouts of complete fecundity suppression were not observed (Fig. 4).

Data for *Bosmina longirostris* are much more limited, both in terms of the length of the time series and demographic detail. Figs. 5 and 6 show fluctuations in total density for the different transfer regimes over a 45-d period for 2-d transfers and a 60-d period for 4-d transfers, respectively. At both food supply rates, populations displayed an initial overshoot in density. With frequent transfer, populations appeared to approach an equilibrium level with only small fluctuations in abundance. For the 4-d transfer cultures, the dynamics differed considerably among replicates: two replicates (Fig. 6b, d) appeared to fluctuate around a level of 4000–5000 individuals/L following the overshoot, and two replicates dropped to very low levels (i.e., <1000 individuals/L). Thus, it is difficult to characterize the dynamics in the 4-d transfer cultures.

Goulden et al. (1982) did not estimate the density of

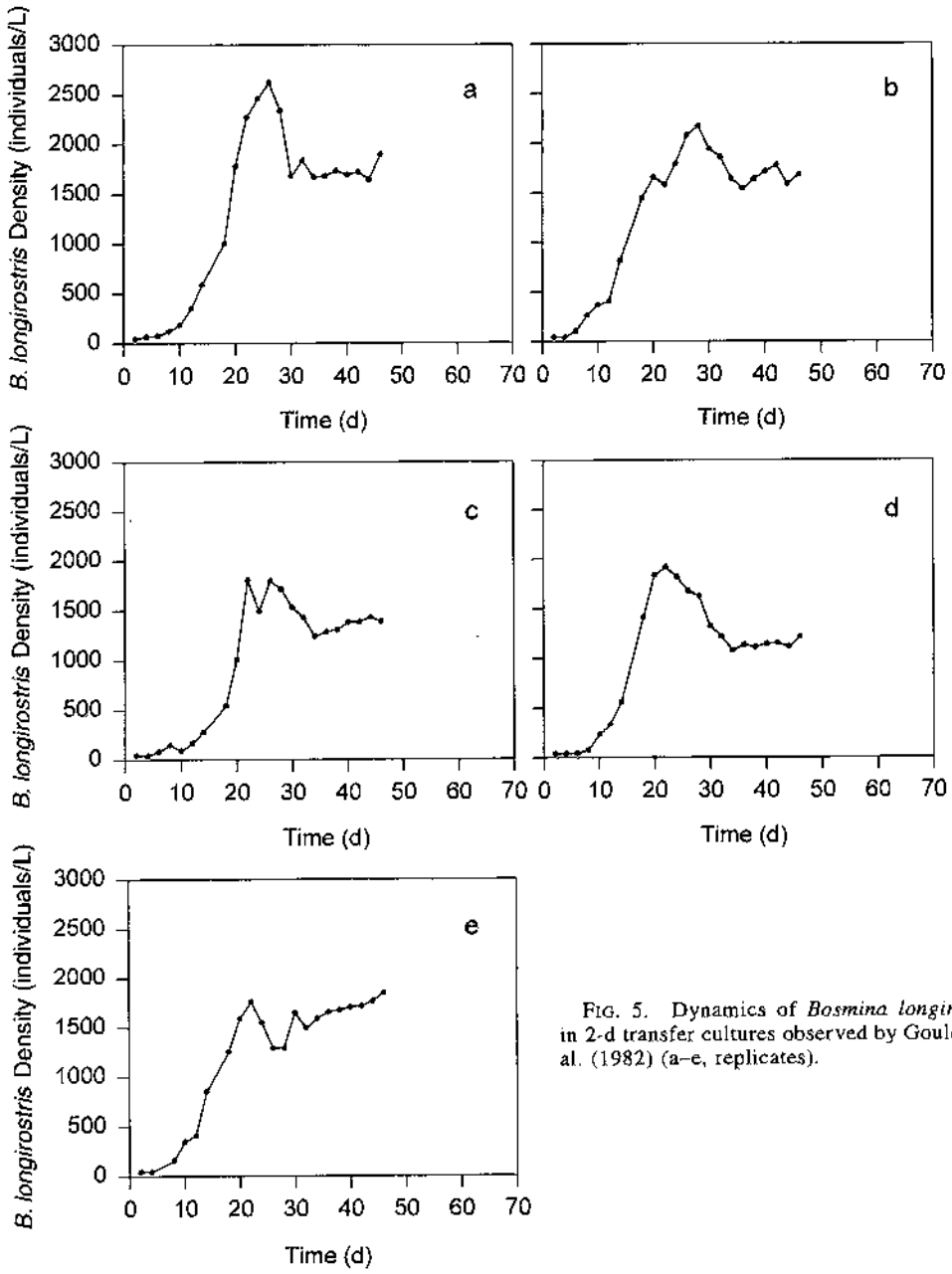

FIG. 5. Dynamics of *Bosmina longirostris* in 2-d transfer cultures observed by Goulden et al. (1982) (a–e, replicates).

juvenile and adult *Bosmina* routinely because of the difficulties in enumerating each group. The snapshot provided on the size structure indicates that juveniles and adults represented an ≈50:50 mix in the populations (Goulden et al. 1982: Fig. 6). No data on the dynamics of fecundity were reported.

Competition experiments were done for both transfer regimes. In the 2-d transfer cultures, *Bosmina* and *Daphnia* coexisted over an ≈70-d period (Goulden et al. 1982: Fig. 4) with *Bosmina* being the numerical dominant. In 4-d transfers (Goulden et al. 1982: Fig. 3), coexistence was also observed over a 60–75 d period, but in this case *Daphnia* dominated the community.

In summary, the experiments by Goulden et al. (1982) provide a range of target data for species raised in isolation and in competition. These data include fluctuations in density, size structure, and, to a limited extent, fecundity. A central feature of these experiments was that food is provided by the experimenter once every few days and these fluctuating food environments represent a formidable challenge for mathematical models. In order to predict correctly per capita birth and death rates, the model must integrate the dy-

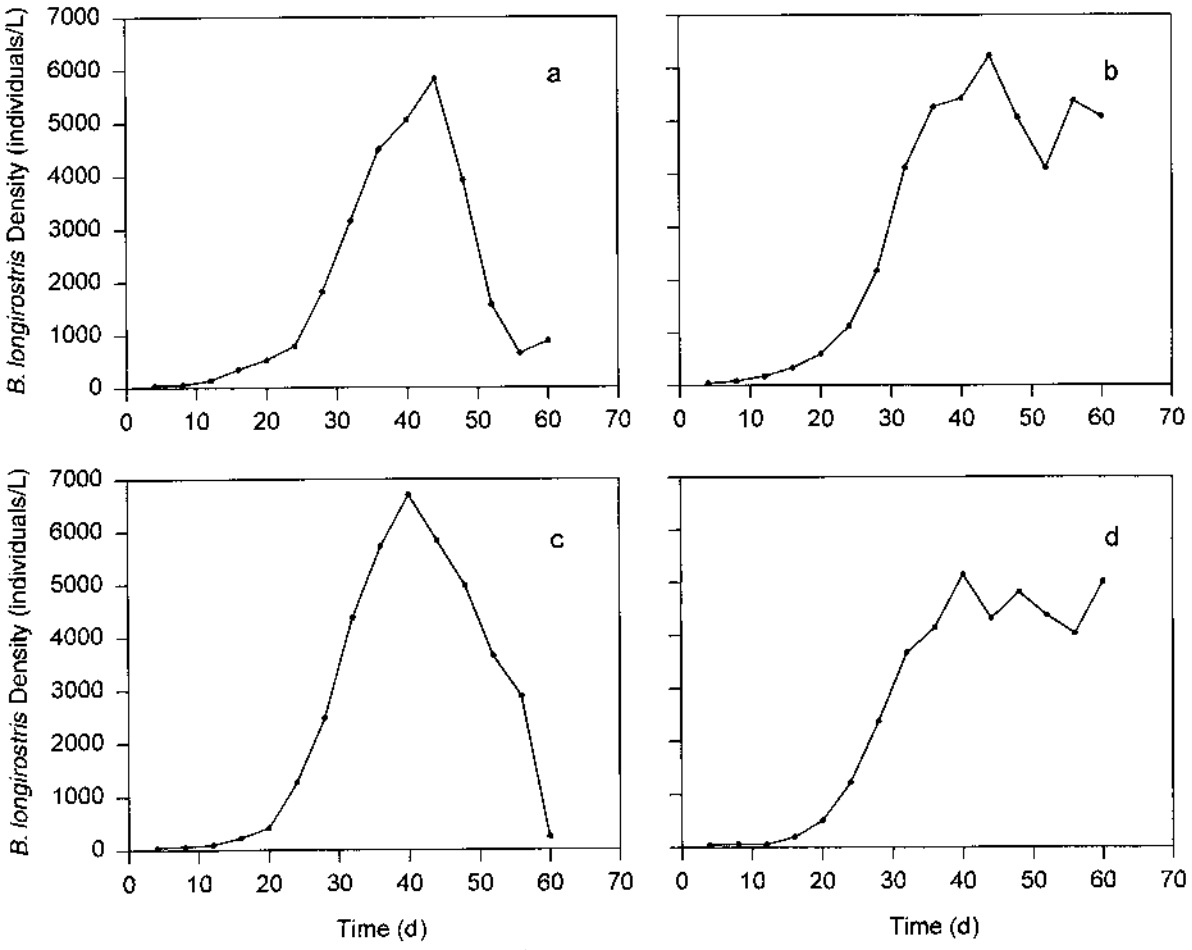

FIG. 6. Dynamics of *Bosmina longirostris* in 4-d transfer cultures observed by Goulden et al. (1982) (a–d, replicates).

namic food environment to predict the performance of individuals in different stages (e.g., juvenile or adult). In the next section, we introduce our stage-structured model and derive parameter estimates for both *D. galeata* and *B. longirostris*.

THE STAGE-STRUCTURED MODEL

Model description and structure

Our stage-structured model was originally developed by Nisbet et al. (1989) to describe *Daphnia pulex*, but no quantitative experimental tests were attempted in that paper. Here, we outline its salient features and refer the reader to the original paper for a more extensive exposition of the biological assumptions.

The model is formulated in the language of delay-differential equations and was constructed using a methodology that has been described in detail elsewhere (Gurney et al. 1983, 1986, Nisbet and Gurney 1983). We recognize three stages in the herbivore population: juveniles (J), immature adults (Y), and reproductively mature adults (A). Juveniles are defined to be individuals who commit, or who have the capacity to commit, all excess assimilate not required for maintenance, to growth. The young adult stage covers the period, roughly two molts in duration, that elapses between achieving capacity for commitment of assimilate to reproduction to the release of the first brood of neonates. The adult stage covers the remainder of the animal's life.

For the juvenile and immature adult stages, we define a development index (or physiological age) such that individuals mature to the next stage when this 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. Changes in the total number of individuals in each stage are determined by a set of a delay-differential equations listed in Table 1. Most of the expressions in Table 1 are consistent with intuition, the only exception being the expression for recruitment to the young adult stage, which is complicated by the fact that the juvenile stage duration may vary over time. The "additional relationships" in Table 1 are derived so as to avoid the need to compute integrals at every step of the numerical solution.

Juveniles and adults feed at a rate given by a type

TABLE 1. The model structure.

Populations

$J(t)$ = Number of juveniles at time t
$Y(t)$ = Number of young adults at time t
$A(t)$ = Number of reproductively mature adults at time t

Rates

$R_J(t)$ = Juvenile recruitment rate at time t
$R_Y(t)$ = Young adult recruitment rate at time t
$R_A(t)$ = Mature adult recruitment rate at time t
$M_A(t)$ = Adult senescence rate at time t

Properties of individuals

$h_J(t)$ = Juvenile development rate at time t
$\delta_J(t)$ = Juvenile per capita death rate at time t
$\beta(t)$ = Adult fecundity at time t
$\delta_A(t)$ = Adult (and egg) per capita death rate at time t

Related functions

$S_J(t)$ = Through-stage survival for juvenile maturing at time t.
$S_Y(t)$ = Through-stage survival rate for young adult maturing at time t.
$S_A(t)$ = Through-stage survival for adult dying by senescence at time t.
$\tau(t)$ = Juvenile development time for individual maturing at time t.

Balance equations

$$\frac{dJ(t)}{dt} = R_J(t) - R_Y(t) - \delta_J(t)J(t) \quad \text{Juveniles}$$

$$\frac{dY(t)}{dt} = R_Y(t) - R_A(t) - \delta_A(t)Y(t) \quad \text{Young adults}$$

$$\frac{dA(t)}{dt} = R_A(t) - M_A(t) - \delta_A(t)A\mathbf{t}) \quad \text{Mature adults}$$

Rates

$$R_J(t) = \beta(t)A(t) \quad \text{Juvenile recruitment}$$

$$R_Y(t) = R_J(t - \tau_J(t))S_J(t)\frac{h_J(t)}{h_J(t - \tau_J(t))} \quad \text{Young adult recruitment}$$

$$R_A(t) = R_Y(t - 2T_M)S_Y(t) \quad \text{Mature recruitment}$$

$$M_A(t) = R_A(t)S_A(t) \quad \text{Adult senescence}$$

Additional relationships

$$S_J(t) = \exp\left\{-\int_{t-\tau(t)}^{t} \delta_J(x)\,dx\right\} \Rightarrow \frac{dS_J(t)}{dt}$$

$$= S_J(t)\left\{\delta_J(t - \tau(t))\frac{h_J(t)}{h_J(t - \tau(t))} - \delta_J(t)\right\} \quad \text{Juvenile survival}$$

$$S_Y(t) = \exp\left\{-\int_{t-2T_M}^{t} \delta_A(x)\,dx\right\} \Rightarrow \frac{dS_Y(t)}{dt}$$

$$= S_Y(t)\{\delta_A(t - 2T_M) - \delta_A(t)\} \quad \text{Young adult survival}$$

$$S_A(t) = \exp\left\{-\int_{t-T_A}^{t} \delta_A(x)\,dx\right\} \Rightarrow \frac{dS_A(t)}{dt}$$

$$= S_A(t)\{\delta_A(t - T_A) - \delta_A(t)\} \quad \text{Adult survival}$$

$$1 = \int_{t-\tau(t)}^{t} h_J(x)\,dx \Rightarrow \frac{d\tau_J(t)}{dt}$$

$$= 1 - \frac{h_J(t)}{h_J(t - \tau(t))} \quad \text{Juvenile development time}$$

TABLE 2. The model functions. In this table the notation $[x]_+ = x$ if $x > 0$ and 0 otherwise. It reflects the fact that juvenile development rate and adult fecundity may never be negative.

Ingestion

$$I_J(t) = \frac{I_{mJ}F(t)}{F(t) + F_h} \quad \text{Instantaneous intake rate per juvenile}$$

$$I_A(t) = \frac{I_{mA}F(t)}{F(t) + F_h} \quad \text{Instantaneous intake rate per adult}$$

$$\bar{I}_J(t) = \int_{t-T_M}^{t} I_J(x)\,dx \quad \text{Average intake rate per juvenile}$$

$$\bar{I}_A(t) = \int_{t-T_M}^{t} I_A(x)\,dx \quad \text{Average intake rate per adult}$$

Functions

$$h_J = \frac{1}{T_{max}} + \left(\frac{1}{T_{min}} - \frac{1}{T_{max}}\right)\left[\frac{\epsilon_A\bar{I}_J - \Gamma_J}{\epsilon_A I_{mJ} - \Gamma_J}\right]_+ \quad \text{Juvenile development}$$

$$\beta = c[\epsilon_A\bar{I}_{mA} - \Gamma_A]_+ \quad \text{Adult fecundity}$$

$$\delta_J = \delta_{J0}\exp\{-\bar{I}_{mJ}/I_{J0}\} \quad \text{Juvenile mortality}$$

$$\delta_A = \delta_{A0}\exp\{\bar{I}_{mA}/I_{A0}\} \quad \text{Adult mortality}$$

II functional response, and this instantaneous intake rate is used to calculate the average intake over an instar of fixed duration (T_M). This average intake is used to determine food-dependent rates of mortality for each stage, and fecundity for the adult stage (Table 2). The development index for juveniles is a function of their age and feeding history, and an important feature to stress is that, while development does depend on the instantaneous intake rate of juveniles, individuals experiencing food levels at or below maintenance levels still develop, albeit at a low rate. This arbitrary assumption removes the possibility of some juvenile individuals developing at extremely low rates yet surviving to produce some eggs, a phenomenon never observed in *Daphnia*, and capable of seriously distorting demographic predictions (Gurney et al. 1996). There is no "maturation mortality" associated with production of the first brood of neonates (see Nisbet et al. [1989]: Eq. 27; our assumption here amounts to setting $S_{JY} = 1$ in that equation).

Food dynamics can be specified for the particular experimental system under study. For example, in Nisbet et al. (1989) we present equations describing logistic prey growth and the presence of a prey refuge. In this paper, we are dealing with an experimental protocol in which food (i.e., a certain number of algal cells representing a known amount of carbon) is provided at discrete intervals and these food cells do not grow or reproduce in the rearing environment. Thus, immediately prior to the transfer of zooplankton individuals, the food is reset in the vessel to a level (F_R) and

TABLE 3. Parameter definitions and estimates for *Daphnia galeata* and *Bosmina longirostris*.

Species	Parameter	Description	Estimate	Source
Daphnia galeata	I_{mJ}	Maximum ingestion rate for juveniles	0.008 mg C/d	4, 7, 12
	I_{mA}	Maximum ingestion rate for adults	0.025 mg C/d	4, 7, 12
	F_h	Half-saturation constant in functional response	0.98 mg C/L	4, 7, 12
	ϵ	Assimilation efficiency	0.6–1.0	12
	Γ_J	Juvenile maintenance rate	0.000187 mg C/d	1, 2, 6
	Γ_A	Adult maintenance rate	0.0008 mg C/d	1, 2, 6
	c	Conversion of energy available for reproduction to neonates (*Daphnia* individuals/mg C)	4045	8
	T_M	Instar duration	2.7 d	8
	T_{max}	Maximum development time for juveniles	20.0 d	5, 8
	T_{min}	Minimum development time for juveniles	2.2 d	5, 8
	I_{0J}	Constant in formula for juvenile mortality rate	0.00035 mg C/d	5, 8
	I_{0A}	Constant in formula for adult mortality rate	0.001 mg C/d	5, 8
	δ_{J0}	Maximum mortality rate: juveniles	0.225 d^{-1}	6
	δ_{A0}	Maximum mortality rate: adults	0.225 d^{-1}	6
	F_{ecmax}	Maximum daily egg production	7.5 d^{-1}	7, 8
Bosmina longirostris	I_{mJ}	Maximum ingestion rate for juveniles	0.00043 mg C/d	4, 10
	I_{mA}	Maximum ingestion rate for adults	0.00071 mg C/d	4, 10
	F_h	Half-saturation constant in functional response	0.18 mg C/L	4, 10
	ϵ	Assimilation efficiency	0.6–1.0	9
	Γ_J	Juvenile maintenance rate	0.000056 mg C/d	3, 11
	Γ_A	Adult maintenance rate	0.000085 mg C/d	3, 11
	c	Conversion of energy available for reproduction to neonates (*Bosmina* individuals/mg C)	9708	10
	T_M	Instar duration	3.0	5, 9
	T_{max}	Maximum development time for juveniles	8.0	9
	T_{min}	Minimum development time for juveniles	1.0	9
	I_{0J}	Constant in formula for juvenile mortality rate	0.000078 mg C/d	5, 9
	I_{0A}	Constant in formula for adult mortality rate	0.00015 mg C/d	5, 9
	δ_{J0}	Maximum mortality rate: juveniles	0.33 d^{-1}	3
	δ_{A0}	Maximum mortality rate: adults	0.33 d^{-1}	3
	F_{ecmax}	Maximum daily egg production	3.0 d^{-1}	9, 10

Sources: 1) Schindler 1968, 2) Lemke and Lampert 1975, 3) Threlkeld 1976, 4) DeMott 1982, 5) Goulden et al. 1982, 6) Tessier et al. 1983, 7) Lynch et al. 1986, 8) Urabe 1988, 9) Urabe 1991*a*, 10) Urabe 1991*b*, 11) Urabe and Watanabe 1990, 12) Urabe and Watanabe 1991.

following transfer of zooplankton (i.e., during the transfer interval) food (F) dynamics are described by:

$$\frac{dF(t)}{dt} = -I_J(t)J(t) - I_A(t)[Y(t) + A(t)],$$

in which I represents the instantaneous intake rate.

Model parameterization

There is a large body of quantitative information on the physiological ecology of freshwater zooplankton. In this section, we describe briefly the estimation of model parameters for *Daphnia galeata* and *Bosmina longirostris*. Parameter estimates along with the literature sources of the data used to determine each estimate are provided in Table 3. The Appendix contains further details on the calculations.

Daphnia galeata.—Individuals are born at 0.38 mm length (Lynch 1980) and reproduce once they have exceeded a length of 1.08 mm (Lynch 1980, Urabe 1988). Growth and development are food dependent (Goulden et al. 1982, Urabe 1988, Urabe and Watanabe 1991). Under a high food regime, individuals develop rapidly (the earliest age at first reproduction is in the range of 6.0–7.0 d; Lynch 1980, Goulden et al. 1982, Urabe 1988) and they can grow to a maximum length of 2.33 mm (Lynch 1980, Urabe 1988). Under a low food regime, development times are longer (the age at first reproduction is 11–15 d; Goulden et al. 1982, Urabe 1988) and individuals reach a maximum size of ≈1.35 mm (Urabe 1988).

To determine stage-specific rates, we adopted a typical length of a juvenile as 0.7 mm, and considered 1.2 mm representative of adults. Since both laboratory and field populations often suppress food levels to extremely low levels, we chose the typical adult lengths from growth curves of individuals being raised at a very low food supply (i.e., equivalent to a C source of 0.05 mg/L).

Non-linear regression was used to estimate the two parameters describing the functional response for both juvenile and adult individuals. While the maximum ingestion rate differed significantly between stages (Table 3), the half-saturation constant (F_h) was not significantly different between juveniles and adults (Appendix). This is consistent with previous results for *Daphnia pulex* (McCauley et al. 1990*b*).

Measured assimilation efficiencies are notoriously variable for cladoceran zooplankton (e.g., Porter et al. 1982, Lynch et al. 1986) with quoted values ranging from 0.6 to >1.0! There are no direct estimates of

assimilation efficiency for *D. galeata* with a low food supply. Urabe and Watanabe (1991) calculated assimilation efficiency from the net carbon balance, but while they measured ingestion and losses due to growth, respiration, and reproduction directly, they did not measure the assimilation rate; thus, assimilation efficiency was only inferred from the energy balance. The only direct measure of assimilation efficiency (i.e., measured as the ratio of assimilation rate to ingestion rate, correcting for respiration losses) for *D. galeata* was made at constant high levels of food by Lynch et al. (1986). Estimates were on the order of 0.6, and did not differ between juveniles and adults. These high food estimates agree well with Urabe and Watanabe's (1991) calculated values for high-food supply rates. Thus, in the absence of direct observation of assimilation efficiency under a low food regime, we will treat this as a free parameter that is bounded between 0.6 and 1.0. Indirect evidence (Urabe and Watanabe 1991) points to values in the range of 0.7–0.8 for low food levels. Based on the evidence from Lynch et al. (1986), we assume that assimilation efficiencies are identical for juveniles and adults.

Daily maintenance costs for juvenile and adult individuals were determined from size-specific respiration data provided by Urabe and Watanabe (1991) and by assuming that individuals require 5% of their body mass for carapace replacement (e.g., Schindler 1968, Paloheimo et al. 1982, Lynch et al. 1986, Gurney et al. 1990, McCauley et al. 1990*a*, Urabe and Watanabe 1991). In calculating the daily cost for the carapace, the molt duration was fixed at 2.7 d (Goulden et al. 1982, Urabe 1988).

A conversion term relating energy available for reproduction to the number of eggs produced was determined from the carbon needed to produce one offspring. Urabe (1988) estimated the carbon present in newly laid eggs and this value was used to calculate the number of eggs produced per unit of carbon available for reproduction. This egg mass was assumed to be fixed since individuals either in lab populations or the field typically experience low food conditions over the time scale of an instar.

Parameterizing mortality provided the most difficult challenge, despite the fact that food-dependent survivorship has been measured often for *Daphnia*. Tessier et al. (1983) measured starvation times for *D. galeata* and these data yield estimates of maximum mortality rates when food supply equals zero. Goulden et al. (1982) observed age-specific survivorship at three different food levels, but because the experiments were intended to measure population growth rates, survivorship at high food was recorded for only 25–30 d. Using these data, we can calculate the mortality rate experienced by the juvenile and adult stage class. In our model, mortality has two components: (1) food-dependent mortality and (2) a maximum adult life-span (T_A). Food-dependent mortality is influenced by the average intake over the previous instar. To estimate the characteristic parameter in the mortality function for juveniles and adults, the natural logarithm of the mortality rate is regressed against the ingestion rate for those food levels calculated from the functional response. The three survivorship curves measured by Goulden et al. (1982) contribute three points at different food levels, and one additional point is provided by the mortality rate observed under starvation conditions (Tessier et al. 1983). Uncertainty comes from the fact that the characteristic slope was determined in some cases by only three points, since mortality rates are zero for juveniles at very high food levels. The final parameter in the mortality function is maximum adult life-span, and the only available estimates come from other *Daphnia* species. Estimates range from 10–40 days.

Thus, although the model is parameter "rich," there are only two parameters (assimilation efficiency and adult life-span) that cannot be directly determined for low food environments typical of laboratory and field situations. In addition, these two parameters are not simply "free"-fitting parameters because they are restricted to biologically plausible ranges based on observations from *D. galeata* or other *Daphnia* spp.

Bosmina longirostris.—*Bosmina* is a much smaller genus than *Daphnia* and, in general, there are fewer observations on its physiological ecology. It is often possible to find multiple studies of key processes for a particular *Daphnia* species (e.g., ingestion, respiration, etc.) or at least work on species of similar size. This allows for a rigorous comparison of estimates among studies that can be very revealing (Gurney et al. 1990, McCauley et al. 1990*a*). For *Bosmina*, however, these cross comparisons are not feasible for most parameters.

Individuals are 0.183 mm in length when born and have a minimum length at first reproduction of 0.274 mm (Lynch 1980, Urabe 1991*a*). In contrast to *Daphnia*, time to first clutch is relatively short (i.e., ≈3–6 days) even with low food supply (Goulden et al. 1982, Urabe 1991*a*). Ultimate adult size is dependent on food supply, but the magnitude of adult growth is much less in *Bosmina* than in *Daphnia* spp (Lynch 1980, Urabe 1991*a*).

We assume the lengths of a typical juvenile and adult to be 0.23 and 0.28 mm, respectively. Non-linear regression shows that estimates of the half-saturation constant do not differ significantly between juveniles and adults, and the maximum ingestion rate for each stage is presented in Table 3. There are no direct observations of assimilation efficiency, but Urabe (1991*b*) calculated an average of 0.925 with a C source of 0.05 mg/L, and with values ranging from 0.9 to 1.0. The daily maintenance rate for each stage is based on size-specific respiration measurements (Urabe and Watanabe 1990, Urabe 1991*a*), and it also assumes a daily

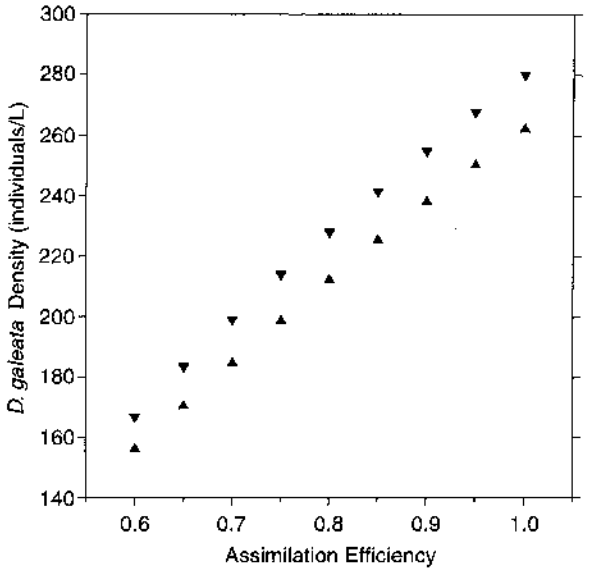

FIG. 7. The effect of changes in assimilation efficiency on "equilibrium" levels of *Daphnia galeata* in 2-d transfer regimes. Model predictions are derived from the upper and lower bounds in total density measured over days 195–200.

molt cost, as in *Daphnia galeata*. The carbon needed to produce a new egg was estimated by Urabe (1991*b*).

Survivorship was estimated at different food levels by Goulden et al. (1982) and Urabe (1991*b*). There are no estimates of starvation times for *Bosmina*, so we used an allometric relationship based on cross-species comparisons developed by Threlkeld (1976) for crustacean zooplankton to determine a representative starvation time for *Bosmina*. The characteristic slope in the mortality function was estimated using six points for both juveniles and adults. Maximum adult life-span falls in the range of 10–30 d (Goulden et al. 1982).

Model Performance

We first examine the ability of the model to capture the dynamics of the single species populations and competing populations when raised in 2-d transfer cultures (i.e., Goulden et al.'s "medium food"), and then assess model performance in the 4-d transfer experiments (Goulden et al.'s "high food").

All parameters (Table 3) were estimated from independent observations of individual performance, and there are only two parameters (assimilation efficiency and adult longevity) for which accurate measurements are unavailable. Values for these parameters, however, are restricted to relatively narrow ranges, and we proceed by assessing whether values within these biologically plausible ranges can yield correct "equilibrium" densities. We then fix the parameters for subsequent tests of model predictions against dynamics of the populations.

Dynamics with 2-d transfers

Daphnia galeata.—The assimilation efficiency has a big effect on predicted equilibrium levels (Fig. 7),

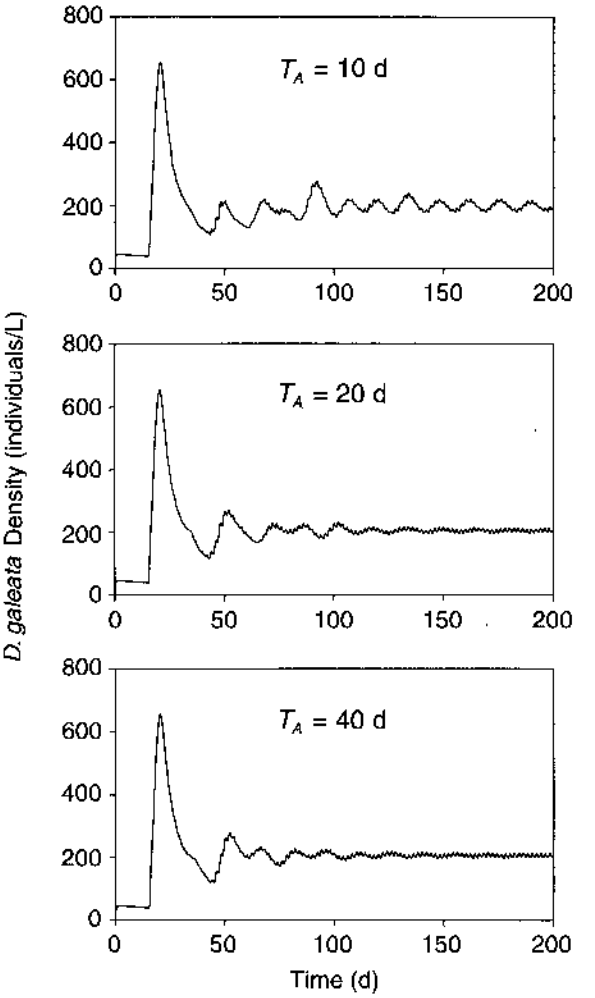

FIG. 8. Dynamics of total density of *Daphnia galeata* predicted by the stage-structured model. Panels show the effect of varying adult longevity (T_A) while holding assimilation efficiency at 0.75. Dynamics for T_A = 30 (not shown) are analogous to those shown for T_A = 40.

while large changes in adult longevity yield only very minor differences (Fig. 8). Because adult longevity has a minimal effect on equilibria, we will examine predictions by holding longevity fixed, and, once the effect of assimilation efficiency is assessed, we will then look at the effects of adult longevity on dynamics. In Fig. 7, upper and lower prediction bounds are shown for each value of assimilation efficiency. The model predicts bounds rather than a single equilibrium value because it generates very small amplitude oscillations in density created by the 2-d food cycle. The model can correctly account for the average levels observed in the cultures if biologically plausible values of assimilation efficiency are adopted in the range of 0.7–0.8. We now fix the value of assimilation efficiency at 0.75 and examine whether the model can capture the population dynamics and how variation in adult longevity affects the dynamics.

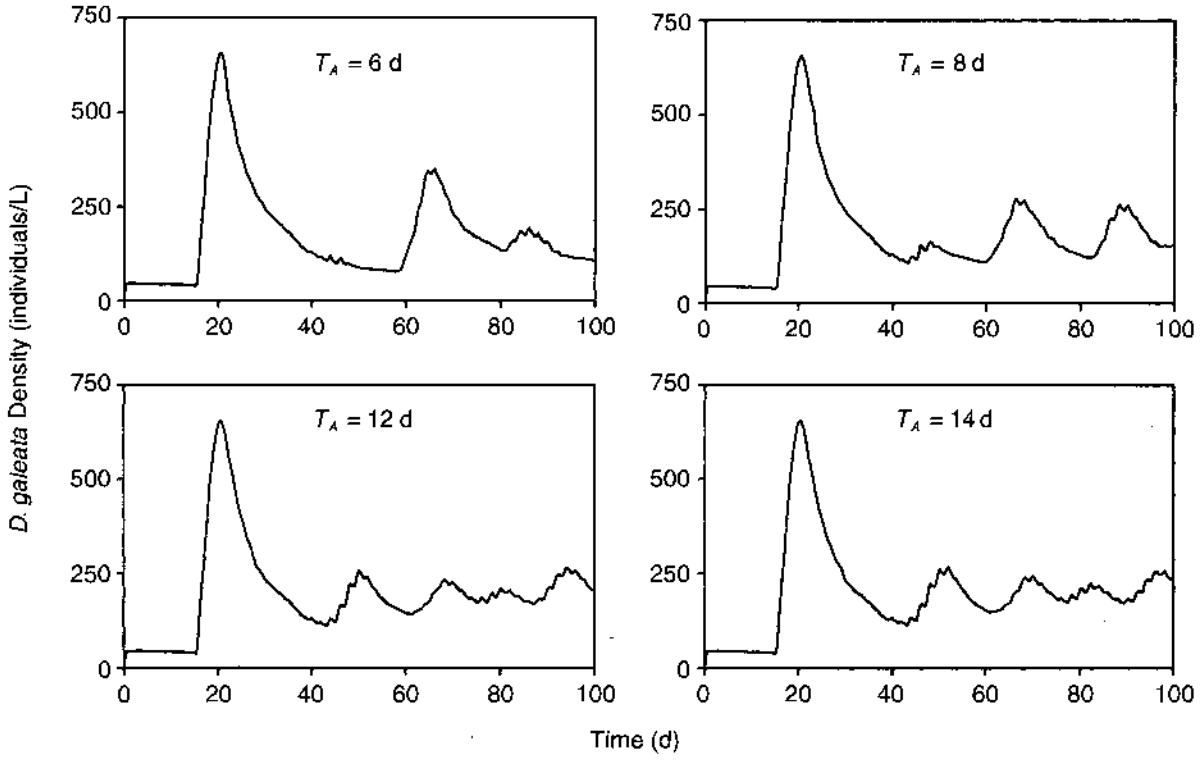

FIG. 9. The effect of small variation in T_A on dynamics of *Daphnia galeata* in the 2-d transfer regime.

Fig. 8 shows the dynamics of the model population at low food over a 200-d period, assuming various adult longevities. All variants predict damped oscillations to an eventual "equilibrium" with very small amplitude cycles reflecting the pulsed food conditions. The transient approach to the equilibrium is complex and does not consist of damped oscillations with a single frequency as is often found in unstructured models. The dynamic features of the oscillations are also affected by adult longevity. These results suggest that the experimental dynamics observed are transient phenomena rather than sustained fluctuations (recall that the experimental period lasted only 65–70 d).

Assuming an adult longevity of ≈10 d (Fig. 8), the model correctly predicts the average dynamics in total density (cf. Fig. 8 and Fig. 1f). The model correctly accounts for the timing and amplitude of the fluctuations in total density of *D. galeata,* and for the interesting feature that following the large initial overshoot, the zenith of the second cycle is smaller than the peak of the third cycle. In the experimental data (Fig. 1), observations from the first three cycles create the impression that further extrapolation of these data would yield sustained cycles (since the amplitude of the cycle appears to be growing), but the model predicts that this effect is not sustained over time and that the oscillations eventually dampen. Unfortunately, the experiment was not run long enough to discern the relationship of subsequent cycle amplitudes. However, the predicted amplitude of the dynamics of the first cycle closely matches the observed dynamics (i.e., peak density and density at the nadir of the first cycle).

Recall that four of the five replicates exhibit a diminished second cycle relative to the first and third cycle (Fig. 1a, c–e) and in the remaining replicate the second and third cycle have similar maxima (Fig. 1b). In one case (Fig. 1c), the second cycle is virtually absent and timing of the third cycle coincides with the other replicates. The range of dynamics observed among replicates can be captured by the model through very minor variation in adult longevity (Fig. 9). Reducing adult longevity slightly, to 8 d, reduces substantially the amplitude of the second cycle, while increasing adult longevity to 12 or 14 d creates dynamics in which the zenith of the second cycle is equal to, or larger, than the third cycle.

The stage-structured model makes detailed predictions about the demography of the observed fluctuations (Fig. 10). It correctly predicts the domination of the *D. galeata* population by juveniles (cf. Fig. 10 and Fig. 3), and it captures many of the dynamic features of fecundity suppression/release and changes in stage structure that produce the fluctuations (cf. Fig. 10 and Fig. 3). Fecundity suppression in the model results from the overproduction of juveniles leading to a negative temporal correlation between juvenile density and fecundity (Fig. 10). Time series analysis for each experimental replicate (Fig. 11) shows that the proportion

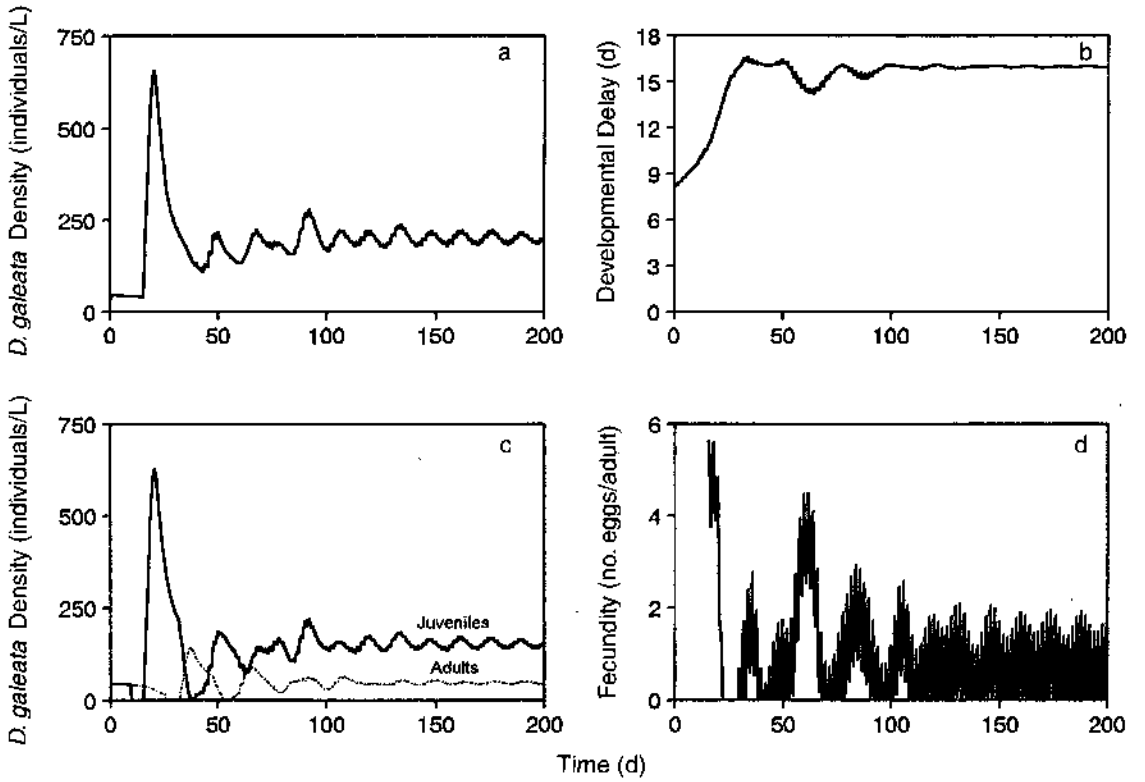

FIG. 10. Detailed model predictions for the dynamics of (a) total density, (b) juvenile stage duration, (c) density of juveniles and adults, and (d) fecundity for *Daphnia galeata* receiving 0.25 mg C every 2 d. Adult longevity is set at 10 d.

ovigerous females (the only index of fecundity) is significantly negatively correlated with the proportion of the population composed of juveniles. These significant negative relationships are maintained even if data from the first cycle are excluded. Early bouts of fecundity release are related to the decline in juvenile density; however, careful inspection of model dynamics shows that as the dynamics in age structure "equilibrate," declines in adult density lead to a bout of fecundity release (e.g., Fig. 10: day 6–75).

Many of the detailed demographic predictions concerning fluctuations in fecundity and age structure cannot be tested because they far exceed the level of detail observed in the real populations. For example, the model predicts interesting dynamics of fecundity suppression/release during successive cycles that leads to the diminished second cycle followed by a larger amplitude third cycle. These mechanisms cannot be evaluated with the existing data, but they suggest new experiments.

Bosmina longirostris.—The duration of observations for the single species cultures of *Bosmina* (Fig. 5) is even shorter than for *D. galeata,* and there is little information on the size structure of the population because of the difficulty in categorizing these small individuals during the census and transfer (Goulden et al. 1982). In addition, there is no information on the dynamics of fecundity.

For *B. longirostris* supplied with low food, the estimated assimilation efficiency is higher (0.9–0.95) than that of *D. galeata,* but still within the biologically plausible range of values inferred for cladocera (Urabe 1991*b*). Even with this assimilation efficiency, the model underpredicts the total density of individuals by ≈20% (Fig. 12). The higher observed values for *Bosmina* in the population experiments may be explained by the ability of this species to browse more efficiently on the bottom of the container and thus yield a higher effective assimilation efficiency compared to *D. galeata.*

The model correctly predicts the initial overshoot in this species and the timing of the first oscillation (Fig. 12b). For values of $T_A > 10$ d, it predicts that, following the initial overshoot, the oscillations are more heavily damped compared with *D. galeata* (cf. Figs. 12 and 5). The limited *Bosmina* data suggest a rapid, almost monotonic, approach to equilibrium following the initial overshoot in most cases (Figs. 5a, c, d), although two series (Fig. 5b, e) indicate the potential for some fluctuations. The model correctly predicts a roughly equal proportion of juveniles and adults in the population (Fig. 13) as reported by Goulden et al. (1982) for one sample. Unfortunately, there are no data on fecundity to test the model prediction that fecundity is relatively high (Fig. 13) at equilibrium in these cultures.

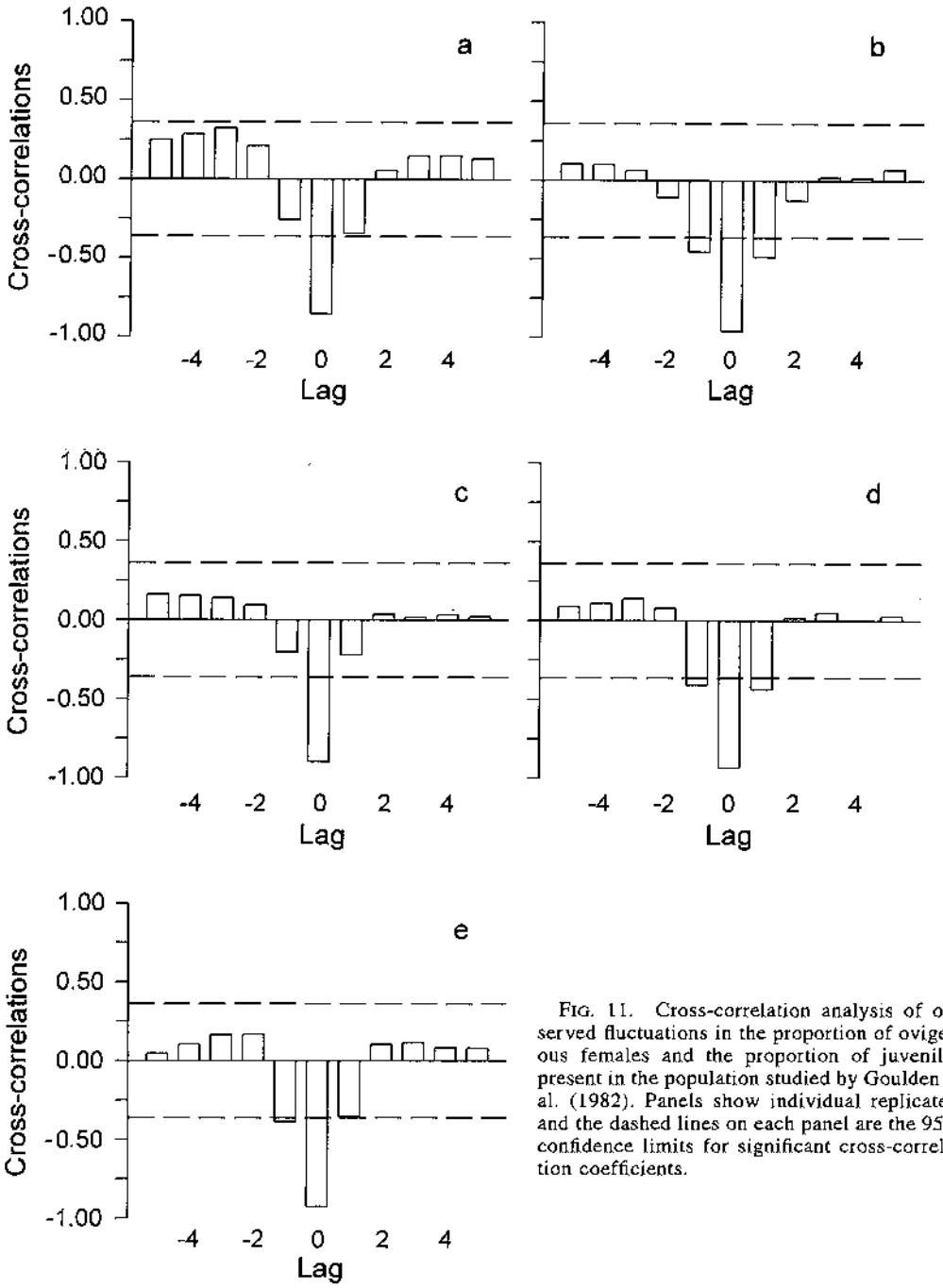

FIG. 11. Cross-correlation analysis of observed fluctuations in the proportion of ovigerous females and the proportion of juveniles present in the population studied by Goulden et al. (1982). Panels show individual replicates, and the dashed lines on each panel are the 95% confidence limits for significant cross-correlation coefficients.

Dynamics of competing populations of Bosmina longirostris *and* Daphnia galeata.—The competition experiments showed that during the experimental period, the two species could coexist at both supply rates of food. In the 2-d transfer cultures, species density fluctuated out of phase and *B. longirostris* had the highest relative density throughout the period. Our model correctly predicts coexistence during the experimental period (Fig. 14) and also correctly predicts that *Bosmina* is the numerical dominant. It further predicts that given sufficient time, *Bosmina* would exclude *Daphnia* in the experiment. It is interesting that the values of assimilation efficiencies adopted to account for the growth of single species raised in isolation correctly predicted coexistence during the experimental period. Other biologically plausible values that yield incorrect levels in single-species cases predict exclusion during this transient period rather than coexistence.

In summary, the stage-structured model did quite

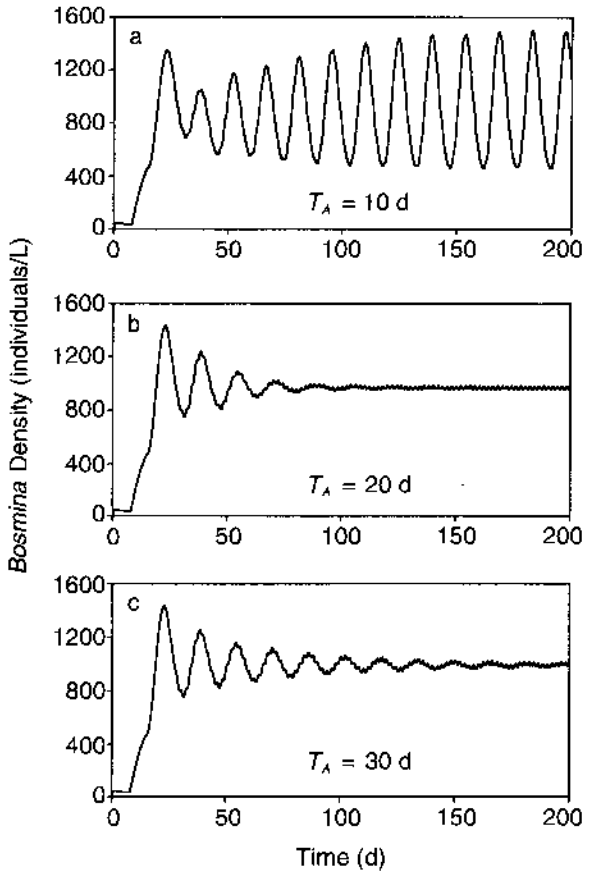

FIG. 12. Model predictions for the dynamics of total density of *Bosmina* in 2-d transfer culture. Panels show the effects of varying T_A with the assimilation efficiency set at 0.925.

well in capturing the dynamics of the populations of *Daphnia* and *Bosmina* raised in isolation and in competition when these populations were transferred to a fresh food universe at 2-d intervals.

Dynamics with 4-d transfers

To examine model performance in predicting the dynamics of population in 4-d transfer cultures, the assimilation efficiencies are fixed for both species at the values adopted for the 2-d transfers. It is unclear how adult longevity might be modified by the change in feeding regime, so this parameter was varied over the plausible biological range.

Daphnia galeata.—Model predictions for the 4-d transfer cultures are at considerable variance with the observed dynamics (cf. Figs. 2 and 15). First, the model overestimates the total density of the population by ≈30–40% assuming no change in assimilation efficiency. Second, while plausible values of adult longevity can yield cycles, the amplitude of which resembles the dynamics of the actual populations (cf. Figs. 2 and 15), the model predicts cycles with a much shorter period. For example, the nadir of the first cycle in Goulden's populations ranges from 40 to 50 d (Fig. 2). By this time, the model displays almost two complete cycles (Fig. 15).

The model also fails to capture changes in demography between 2-d and 4-d transfer schedules. The proportion of juveniles in the 4-d transfer cultures decreased relative to 2-d transfers, and the model does not capture this shift. However, it does correctly predict less severe bouts of fecundity suppression/release (cf. Figs. 4 and 16). Fecundity fluctuates, but is never suppressed to the same degree as in the 2-d transfer cultures.

Bosmina longirostris.—As mentioned previously, it is difficult to characterize *Bosmina*'s dynamics in the 4-d transfer cultures because of the radical divergence among replicates and the short time series of observations (Fig. 6). For plausible values of adult longevity, the model predicts (Fig. 17) the general pattern of fluctuation (i.e., an initial overshoot) but it fails to predict quantitative aspects, in an identical manner to its failure for *Daphnia galeata* in 4-d transfers. The model considerably overestimates the total density of the populations and the period of the cycle is much too short compared to the observed dynamics.

Dynamics of competing populations of Bosmina longirostris *and* Daphnia galeata.—Goulden et al. (1982) observed coexistence of the two species in the 4-d transfer experiments, with *D. galeata* being numerically dominant. While the model correctly predicts the shift in dominance to *D. galeata*, it fails to capture the coexistence of the two species (Fig. 18); it predicts that *D. galeata* should rapidly exclude *Bosmina* over the course of the experimental period, and reducing the assimilation efficiency to its lowest plausible value for *D. galeata* cannot produce coexistence.

In summary, the stage-structured model did poorly in predicting the population dynamics of *D. galeata* and *Bosmina*, and the outcome of competition between *D. galeata* and *B. longirostris* in 4-d transfer culture experiments.

DISCUSSION

The stage-structured model, parameterized using independent physiological and life history data, had considerable success in predicting the dynamics of *Daphnia* and *Bosmina* when food transfers were relatively frequent. Test data for *Daphnia* were the most extensive, and the model correctly predicted many features of the dynamics of total density and age structure by capturing accurately the mechanism of fecundity suppression/release. Despite the fact that individuals in these populations experienced a highly dynamic food environment, the integration of ingestion rates over the molt duration seemed to provide sufficient feeding history to determine correctly rates of development, fecundity, and mortality. The model provided novel explanations for some quantitative features of the cycles (i.e., temporal changes in cycle amplitudes) and for variation observed among replicate *Daphnia* popula-

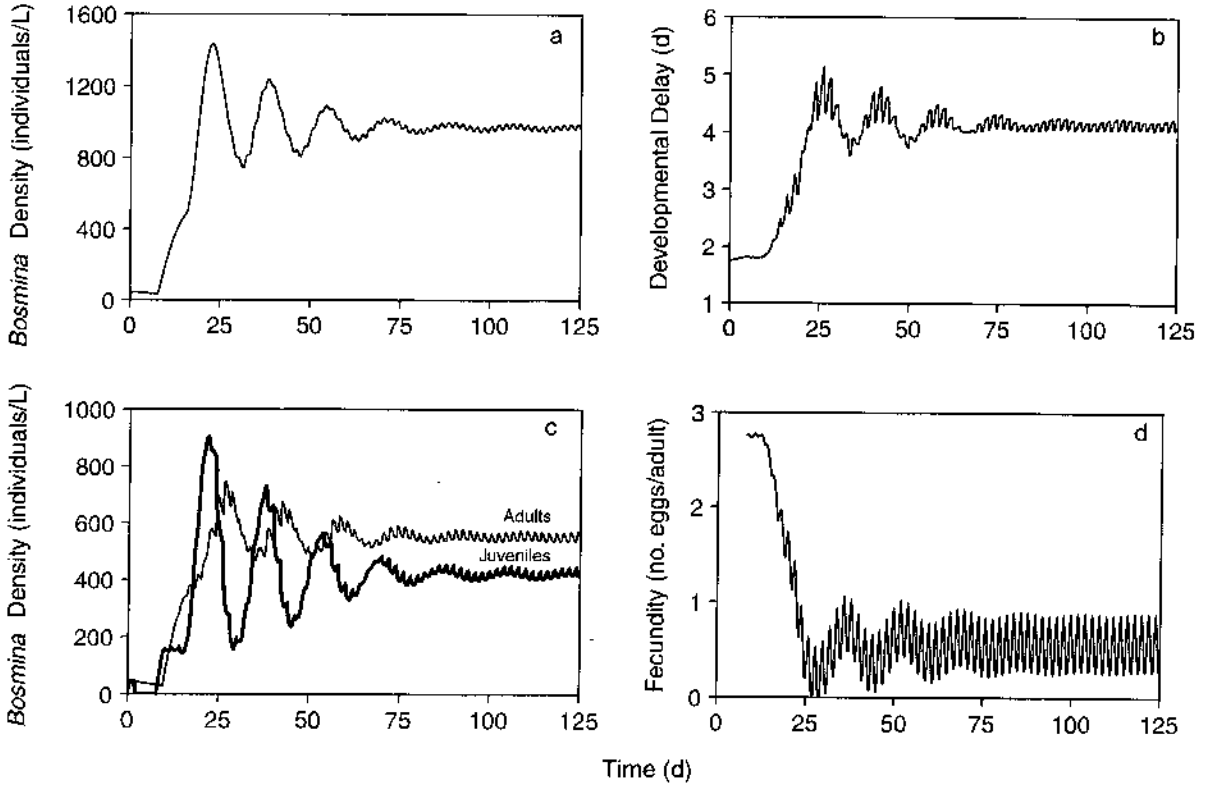

FIG. 13. Detailed model predictions for *Bosmina* in 2-d transfer cultures: (a) total density; (b) juvenile stage duration; (c) density of juveniles and adults; (d) fecundity.

tions. Finally, the model correctly predicted the coexistence of *Daphnia* and *Bosmina* and the numerical dominance of *Bosmina* in the competition experiments.

These successful predictions for 2-d transfer cultures contrast markedly with failures for 4-d transfer conditions, and these failures are instructive. The model success for short transfer intervals suggests that the reason for failures at longer intervals probably was not the result of incorrect parameterization; parameter estimates were derived from independent observations gleaned from the literature and, despite the fact that it is very likely that there were genetic differences between individuals used to determine model parameters and those individuals used in the lab population experiments, parameter estimates were sufficiently accurate to capture dynamics during frequent food transfers. More likely, the models failed because individuals in the long-interval transfer cultures experienced a significant starvation period (relative to molt duration) and the structural rules of the model cannot account for the impact of relatively long starvation intervals on performance of individuals. During bouts of starvation, individual *Daphnia* or *Bosmina* meet maintenance costs from internal reserves that must be replenished after transfer to fresh food. Thus a bout of starvation produces a tax on future assimilate that must ultimately influence both growth and reproduction. This is not incorporated in the model, which predicts, incorrectly, that juveniles experiencing intermittent starvation conditions will still develop, albeit at a minimal rate, and that shortly after being re-introduced to food their development rate will increase without any need to com-

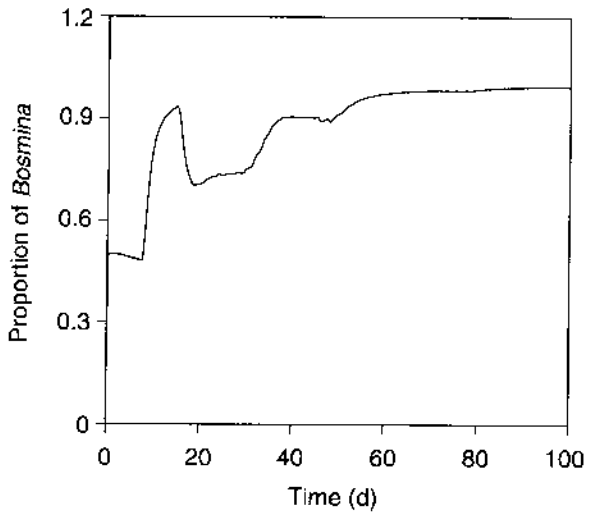

FIG. 14. Model predictions for the competition experiments (2-d transfers) between *Daphnia* and *Bosmina*. The proportion of the two populations represented by *Bosmina* is presented.

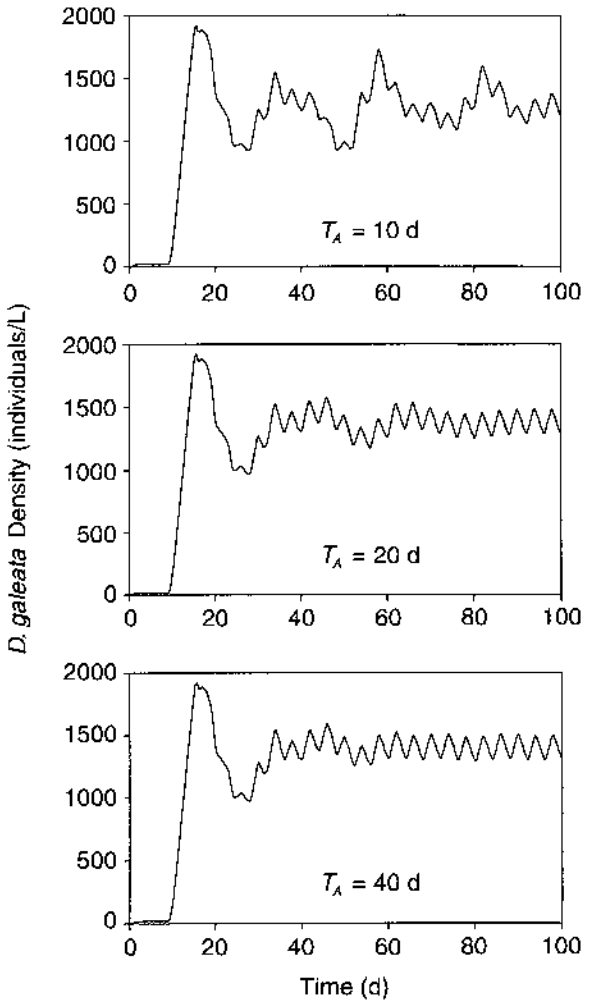

FIG. 15. Dynamics of total density of *Daphnia galeata* predicted by the model for 4-d transfers. Panels show the effect of varying T_A. Dynamics for T_A = 30 d (not shown) are analogous to those shown for T_A = 40.

pensate the losses during the preceding starvation period. Similarly, the model incorrectly allows adults, reintroduced to food following a long bout of starvation, to resume reproduction without replenishing reserves. One result of both of these features is that the "time scale" for model dynamics (i.e., time to first peak, time between successive peaks) is faster at long transfer intervals in the model than was observed by Goulden et al. (1982).

While these physiological mechanisms could be incorporated into stage-structured models, the numerical analysis of the models would be both cumbersome and tricky. A more efficient approach is to construct individual-based models (e.g., De Angelis and Gross 1992, Murdoch et al. 1992) that consider explicit energetic rules for an individual and treat the population as an ensemble of individuals. We are pursuing this alternative theoretical approach and are currently conducting the necessary experiments on the dynamics of starvation and recovery in individuals needed to test energetic rules concerning the dynamic allocation of assimilate following bouts of starvation (Gurney et al. 1990, McCauley et al. 1990).

The current model successfully predicted the outcome of competition between the species for the 2-d transfer culture over the experimental period (i.e., 60–80 d). The model predicts, however, that competitive exclusion would be the ultimate outcome for experiments of longer duration (i.e., >125 d). Goulden et al. (1982) concluded that the oscillatory tendency of the *Daphnia* populations, because of time delays, was crucial for coexistence of the herbivore species. However, the transfer experiments also represent fluctuating food environments, and coexistence under fluctuating conditions is a well-known theoretical alternative (e.g., Hsu et al. 1978, Levins 1979, Armstrong and McGehee 1980). To investigate these explanations, we constructed an analogous unstructured population model for both herbivore species (i.e., a model without stage structure and time delays), and studied its dynamics under transfer conditions. We found that coexistence under transfer conditions is possible for *Daphnia* and *Bosmina* (Nisbet et al. 1996), and this suggests that features associated with the stage-structured development, mortality, and reproduction of the herbivores are not ultimately responsible for coexistence per se, although these features may play an important role in the transient dynamics. Experiments of longer duration (≈150 d) are needed to test these alternative explanations, and also to examine the detailed dynamics in single-species cultures with short transfer intervals as the populations approach "equilibrium."

While the possibility of coexistence in a fluctuating food supply is well known (e.g., Hsu et al. 1978, Levins 1979, Armstrong and McGehee 1980), it is interesting to note that the time scale for the fluctuations of food in batch cultures is much less than the time scale typically set by internally generated consumer resource dynamics or externally driven seasonal fluctuations. Could fluctuations on this time scale be observed in natural systems? Maybe not over time, but perhaps over space (i.e., spatial variation in algal levels encountered during vertical migration) and this suggests that even if vertical migration were driven primarily by the effects of predators (e.g., Zaret and Suffern 1976, Lampert and Taylor 1985, Dini and Carpenter 1992), the variation in food levels encountered by the herbivore species during migration may be sufficient to promote coexistence without habitat partitioning.

While the model successfully predicted the outcome of competition between the species for 2-d transfer culture, it failed for the 4-d transfers, although it did correctly predict that the numerical dominance would switch in favor of *Daphnia* in the 4-day cultures. According to the model, the food supply in the 4-d transfers would be drawn down to very low levels in ≈1–

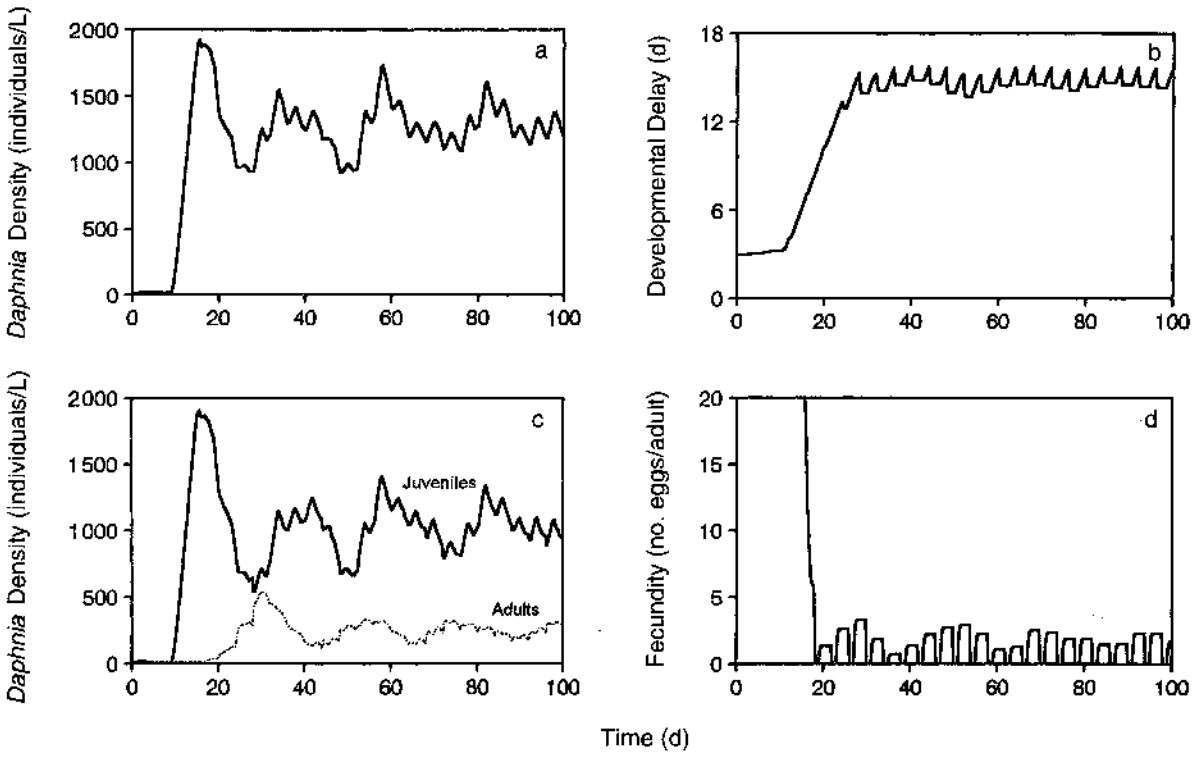

FIG. 16. Detailed model predictions for *Daphnia* in 4-d transfer cultures: (a) total density; (b) juvenile stage duration; (c) density of juveniles and adults; (d) fecundity.

2 d in the presence of *Daphnia*, and this should imply that individuals would experience starvation conditions for at least 2 d. It is possible that the reason *Bosmina* was eliminated in model competition involves an inaccurate representation of starvation mortality for *Bosmina*. The mean starvation time for *Bosmina* is estimated at ≈3–3.5 d. This is used to determine the maximum mortality rate in our food-dependent function. Individuals in our model experiencing food supplies that cannot meet maintenance costs suffer mortality at a maximal rate, following the exponential mortality function. It is likely that the probability of starvation mortality increases sharply after the mean survival time, but is low over shorter time intervals. Thus our representation of mortality possibly overestimated starvation mortality in *Bosmina*.

Another possibility, however, is that there was a mismatch between food available in the cultures and the food supply specified in the model because of experimental artifacts. The water was replaced once every 4 d in the experiments, and it is quite possible that populations of bacteria could increase substantially during the transfer interval. High bacterial growth rates could be sustained at 20°C from corpses and shed carapaces of *Daphnia* and *Bosmina* that litter the floor of the beaker. Perhaps *Bosmina* utilized this bacterial carbon source (Porter et al. 1983, Vaque and Pace 1992) to reduce food-dependent mortality more efficiently than *Daphnia*.

The success of the model in predicting herbivore dynamics opens up two exciting avenues of research previously described by McCauley et al. (1990*a*) and Murdoch et al. (1992). First, we can systematically strip back features in the model to investigate which structural aspects are germane for successful predictions. Our goal is to arrive at the simplest model that can capture the essential dynamic features. For example, what aspects of the model are crucial for predicting the dynamic features of cycles in single-species culture or, as partially answered above for batch culture dynamics, is the description of development or stage structure crucial for predicting the coexistence of *Daphnia* and *Bosmina*? Second, we can systematically add biological realism by considering experimental situations in which prey are dynamically coupled to herbivores rather than being controlled by the experimentalist. This is a crucial next step. We can predict how dynamics should change under laboratory conditions involving *dynamic* single-species edible algal prey. Since the model correctly integrated herbivore energetics under "nongrowing" food conditions, model success or failure under dynamic coupling would test the ability of the model to capture the *Daphnia*–food interaction and the dynamics of prey in the absence of herbivores. Testing the model under these laboratory conditions would help to focus hypotheses put forward to explain the mismatch between theory and field results concerning the absence of "prey-escape" or "paradox of enrich-

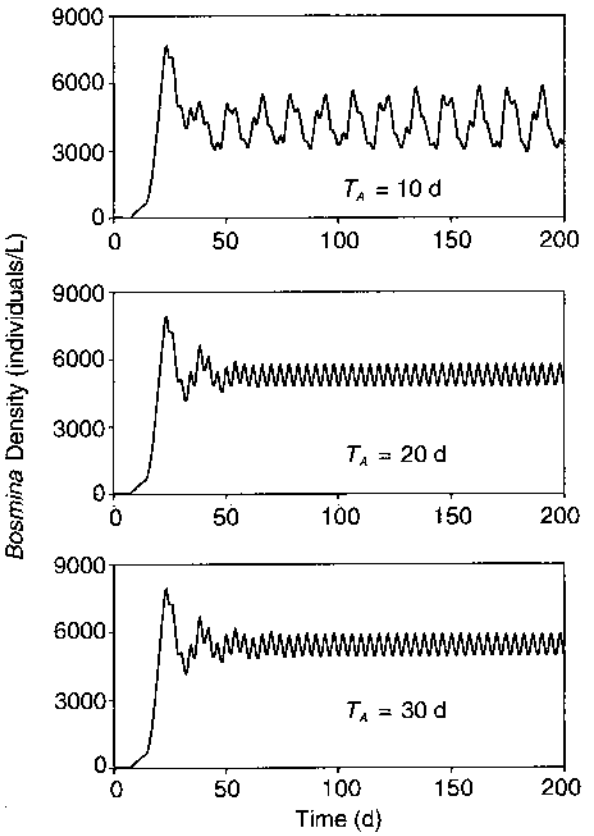

FIG. 17. Dynamics of total density of *Bosmina* predicted by the model for 4-d transfers. Panels show the effect of varying T_A.

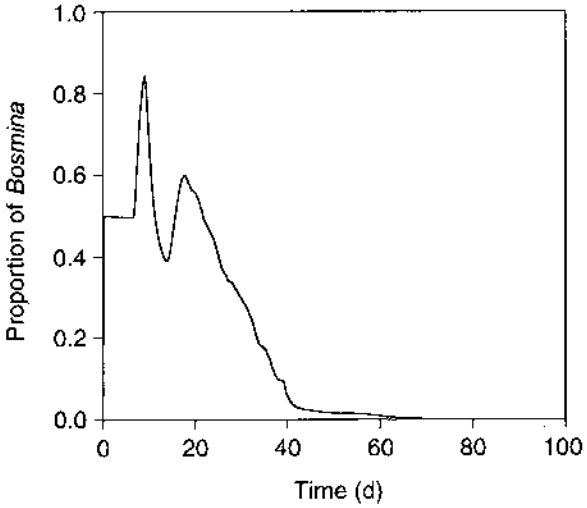

FIG. 18. Model predictions for the competition experiments (4-d transfers) between *Daphnia* and *Bosmina*. The proportion of the two populations represented by *Bosmina* is presented.

ment" cycles (McCauley and Murdoch 1990, de Roos et al. 1992; W. W. Murdoch, R. M. Nisbet, E. McCauley, A. M. de Roos, and W. S. C. Gurney, *unpublished manuscript*).

The level of prediction afforded by these models frequently surpasses existing population level experimental results, and this actually promotes a stronger link between theory and experiment. The structured model provides detailed predictions on the dynamics of fecundity and age structure, and this demographic detail allows for alternative mechanisms producing dynamic behavior to be distinguished experimentally. For example, the model suggested a new mechanism that can account for the variation among replicates observed by Goulden et al. that is testable directly by conducting further population experiments, or indirectly by raising individuals in isolation under a varying food supply to estimate adult longevity. The cost for this detailed level of prediction is borne by the requirement for process-oriented data on the physiological ecology of individuals composing the population, and also results in models that are seemingly "parameter-rich." But it could be argued that since parameter estimates for structured models are arrived at from a synthesis of independent quantitative data on the development, reproduction, and mortality of individuals, these models are actually "parameter-sparse" from the perspective of "free-fitting" parameters. Given that the empirical observations underlying the parameters, in many cases, provide interval estimates, it would be instructive to investigate how minor variation in parameters within these intervals influence model fit. These analyses might suggest potential experiments involving key parameters that significantly influence dynamics.

Our stage-structured model certainly has many structural features that are shared by a wide variety of organisms: rates of energy acquisition and utilization scale with body size, delays in development, and fecundity and mortality depending upon feeding history. The availability of process-oriented data on the physiological ecology of species is burgeoning. These data will enable structured population models, such as ours or simpler variants (Gurney et al. 1996), to be parameterized for a broader range of organisms with a minimal number of "free-fitting" parameters. These models integrate individual-based information and could be used to predict dynamics of single-species and multispecies interactions under a range of environmental conditions.

ACKNOWLEDGMENTS

We thank Clyde Goulden for many suggestions and for providing original data from Goulden et al. (1982) so that they could be replotted accurately to test model predictions. This research has been supported by grants from National Sciences and Engineering Research Council of Canada (NSERC), National Science Foundation (grant number DEB-9319301), and U.S. Environmental Protection Agency (grant number R819433-01-0). Edward McCauley also received International Fellowships from NSERC and the Netherlands Organization for Scientific Research. We thank Vanyee Leung and Michael Vander Meulen for their patient technical support.

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APPENDIX

Detailed Calculations of Parameter Values

Daphnia galeata.—For parameterization of the stage-structured model, we collated data on *Daphnia galeata* Sars 1864 and the subspecies *D. galeata* Sars *mendotae* BIRGE 1918. Urabe and Watanabe (1991) measured ingestion rates (I) vs. length for three food carbon concentrations (0.05, 0.25, and 2.5 mg/L), and Lynch et al. (1986) provided a separate relationship for a C concentration of 1.54 mg/L. These regressions were used to calculate the ingestion rates for typical juveniles (0.7 mm long) and adults (1.2 mm long). Since *D. galeata mendotae* represents a geographical subspecies of similar size and shape to *D. galeata*, we assume that parameter estimates should be similar for both *D. galeata* and *D. galeata mendotae*. Comparison of observations of life history features and rates of energy acquisition from studies on *D. galeata* and *D. galeata mendotae* supported this assumption.

Parameter estimates provided by non-linear regression analysis indicate that the half saturation constant of ingestion rate (F_k) for juveniles (0.98 mg C/L ± 0.4; 95% CI) is not significantly different from the adult estimate (0.99 mg C/L ± 0.3), while estimates of I_{max} (maximum ingestion rate) differ significantly ($P < 0.05$) between juveniles and adults (0.008 mg C/d and 0.025 mg C/d, respectively). The resultant equations for ingestion rates as a function of food concentration (F) for juveniles (I_J) and adults (I_A) are:

$$I_J = 0.008\frac{F}{F + 0.98} \quad \text{and} \quad I_A = 0.025\frac{F}{F + 0.98}.$$

These equations were used to calculate ingestion rates of juveniles and adults for food concentrations used in survivorship experiments reported by Goulden et al. (1982). Mortality rates (δ) were determined from the survivorship curves, and the maximum food-dependent mortality rate (0.228 d^{-1}) was estimated from the starvation of time of 105 h observed by Tessier et al. (1983). The data used to estimate the characteristic slope in the mortality function (Tables 1 and 2) are provided in Table A2. Estimates of I_{0J} and I_{0A} are obtained as the inverse of the slope of the relationship between ln (Mortality rate) vs. Ingestion rate.

Daily maintenance rates (in milligrams of C per day) of juveniles and adults are based on two costs (McCauley et al. 1990*a*): (1) the daily basic maintenance rate (β) and (2) the daily cost of producing a carapace required at the next molt. The daily basic maintenance rate (in inverse days) is the proportion of juvenile (W_J) or adult (W_A) body mass (in milligrams of C) "burned" per day to support the individual, and it is estimated from data on starvation time. According to Tessier et al. (1983), *D. galeata* take 105 h to starve (starvation time, τ_s) on average. If we assume that death from starvation ensues when an individual loses 50% of its initial (W_0) body mass (Lemke and Lampert 1975, Elendt 1989) then we can estimate β from the following formula:

$$\frac{W_{\tau_s}}{W_0} = 0.5 = e^{-\beta\tau_s};$$

thus

$$\beta = \frac{-\ln(0.5)}{\tau_s} = \frac{0.693}{4.375} = 0.158 d^{-1}.$$

TABLE A1. Data used to calculate ingestion parameters for *D. galeata*.

Carbon concentration of food (mg/L)	Juvenile ingestion rate (μg C/d)	Adult ingestion rate (μg C/d)
0	0	0
0.05	0.63	1.73
0.25	1.76	4.44
1.54	3.9	17.0
2.5	6.44	16.6

TABLE A2. Data used to calculate mortality rate parameters for *D. galeata*.

Carbon concentration of food (mg/L)	Juvenile ingestion rate (I_J) (mg C/d)	Juvenile mortality rate (δ_J) (d^{-1})	Adult ingestion rate (I_A) (mg C/d)	Adult mortality rate (δ_A) (d^{-1})
0	0	0.228	0	0.228
0.04	0.00031	0.0519	0.00098	0.058
0.2	0.00136	0.008	0.00424	0.0037
10	0.00729	0	0.02277	0

Following Urabe and Watanabe (1991), the mass of a carapace is assumed to be 5% of the body mass for juveniles (W_J) and adults (W_A). The daily cost to replace the carapace for a juvenile or adult is $1/T_m$ multiplied by the mass of the respective carapace. The molt duration T_m was fixed at 2.7 d (Goulden et al. 1982, Urabe 1988). Thus, the daily maintenance rate for juveniles (Γ_J) and adults (Γ_A) is:

$$\Gamma_J = \beta \cdot W_J + (1/T_m)(0.05W_J)$$

and

$$\Gamma_A = \beta \cdot W_A + (1/T_m)(0.05W_A).$$

The body masses (in milligrams C) for an individual of length 0.7 mm and an individual of length 1.2 mm were determined using the length (l)–carbon-mass relationship ($W = 0.002729\ l^{2.536}$) from Urabe and Watanabe (1991), derived using individuals raised under the low food regime and measured just after the molt (eggs removed from adults).

Bosmina longirostris.—Ingestion rates for typical juveniles (0.23 mm long) and adults (0.28 mm long) were derived from experiments reported by Urabe (1991*b*).

TABLE A3. Data used to calculate ingestion parameters for *Bosmina*.

Carbon concentration of food (mg/L)	Juvenile ingestion rate (μg C/d)	Adult ingestion rate (μg C/d)
0	0	0
0.05	0.094	0.140
0.10	0.132	0.195
0.25	0.288	0.445
2.5	0.397	0.602

TABLE A4. Data used to calculate mortality rate parameters for *Bosmina*.

Carbon concentration of food (mg/L)	Juvenile ingestion rate (I_J) (mg C/d)	Juvenile mortality rate (δ_J) (d^{-1})	Adult ingestion rate (I_A) (mg C/d)	Adult mortality rate (δ_A) (d^{-1})
0	0	0.33	0	0.33
0.04	7.9 E-5	0.149	0.00013	0.149
0.05	9.4 E-5	0.074	0.00015	0.058
0.1	0.00015	0.026	0.00025	0.029
0.2	0.00023	0.020	0.00037	0.026
10	0.00043	0.016	0.00070	0.024

These data yield estimates for F_h of 0.179 and 0.182 mg C/L for juveniles and adults using non-linear regression. Maximum ingestion rates were 0.00043 and 0.00071 mg $C \cdot L^{-1} \cdot d^{-1}$ for juveniles and adults, respectively. Since the values of F_h were not significantly different, a value of 0.18 mg C/L was adopted.

The ingestion functions were then used to estimate ingestion rates experienced by representative juveniles and adults during survivorship experiments reported by Urabe (1991*a*) and Goulden et al. (1982). Unfortunately, no data on starvation times are available for *Bosmina longirostris*. The general regression reported by Threlkeld (1976) for crustacean zooplankton was used to estimate the starvation time for adult *Bosmina* ($\tau_s = 3$ d).

Daily maintenance rates were calculated, as described for *D. galeata*, using an estimate of $\beta = 0.23\ d^{-1}$ derived from the starvation time, molt duration $T_M = 3.0$ d (Urabe 1991*a*), and a mass (in milligrams of C)–length (length in millimetres) relationship of $W = 0.00959\ l^{2.568}$.