

DYNAMICS OF A STRUCTURED SLUG POPULATION MODEL IN THE ABSENCE OF SEASONAL VARIATION

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We develop a novel, nonlinear structured population model for the slug *Deroceras reticulatum*, a highly significant agricultural pest of great economic impact, in both organic and non-organic settings. In the absence of seasonal variations, we numerically explore the effect of life history traits that are dependent on an individual's size and measures of population biomass. We conduct a systematic exploration of parameter space and highlight the main mechanisms and implications of model design. A major conclusion of this work is that strong size dependent predation significantly adjusts the competitive balance, leading to non-monotonic steady state solutions and slowly decaying transients consisting of distinct generational cycles. Furthermore, we demonstrate how a simple ratio of adult to juvenile biomass can act as a useful diagnostic to distinguish between predated and non-predated environments, and may be useful in agricultural settings.

Keywords: Slugs; structured population model; numerical integration.

1. Introduction

Slug damage is a major problem in agriculture and horticulture. It is essential to gain a complete understanding of slug population dynamics for efficacious yet

ecologically harmonious control strategies. The optimisation of the biocontrol of slugs using commercially available nematode parasites^{30,40} (particularly for organic farming practice) is an issue of recent scientific debate. Although a large number of different species of slug are found amongst agricultural crops in Britain, the majority of the damage is caused by *Deroceras reticulatum*, estimated at approximately 70%, both in terms of biomass and numbers.¹⁰ Moreover, this species is a pest of global economic importance,³⁵ and is thus the one we study here. *D. reticulatum* does not have a regular annual breeding cycle, unlike most other common British slugs. This aspect of its life cycle is responsible, perhaps, for its dominance and exacerbates the difficulties in trying to understand and predict population numbers.

The suitability of a particular modelling technique for a given situation will depend on which aspects of a system are deemed most important. The use of age and/or size structured models allows for the explicit and proper inclusion of complex factors in the life cycle of a population. Furthermore, the recent growth in computer capacity and speed has renewed interest in both their development and application.

The most important factors in the life cycle dynamics of *D. reticulatum* are individual size and the prevailing environmental conditions. For example, an individual slug is usually capable of reproducing once it has attained a certain size (indicating maturity) but will, in practice, only lay eggs when conditions are favourable. This makes the situation more complex than for other species where individuals lay eggs mostly at the same time.

While seasonal variations are inherently important,^{13,29} as a first step it is appropriate to consider the dynamics of populations in their absence. Such modelling also has a direct application to those environments inhabited by *D. reticulatum* where there is relatively little variation in climatic conditions, such as agriculture under glass. For situations where growth is dependent only upon size (and not time), size-structured models may be reduced, at least implicitly, to age-structured models. In general non-autonomous regimes however, size and age structure are not simply related and so we maintain a size structured approach throughout in order to provide a natural structure for extending the work to temporally varying life factors.

In the remainder of this section we briefly describe key structured population models from the literature and the numerical methods that have been used to simulate them. In Sec. 2 we explicitly construct detailed functional responses for the model of *D. reticulatum*, keeping the terms as simple as possible while maintaining biological relevance. Section 3 introduces the numerical scheme and model parameters, the latter based on laboratory and field data where possible. Model behaviour is fully investigated and results are discussed in Sec. 4.

1.1. *Slug population dynamics*

Although experimental evidence indicates that there are significant oscillations in slug numbers^{19,35} over long time scales, these appear irregular,¹⁷ and not easily predictable. In general, the underlying dynamics of slugs are not well understood.

A number of models for slug populations have been developed — with some agreement — including delay differential models,²⁹ and a discrete model based on egg production,²⁸ where it has been shown that relatively simple dynamics may generate some of the observed complex behaviour. Schley and Bees³⁰ further explored the effects of time delays on a non-autonomous host-parasitoid model for the interaction between slugs and a dedicated parasitic nematode, and concluded that life stage dynamics are inherently important, the understanding of which is a prerequisite for the exposition of biocontrol measures. Previous models of slug populations which consider life stages have focused on the effects of environmental variations, including crop dynamics, but have not incorporated the effects or dynamics of predators. Shirley *et al.*³¹ used an individual based model to investigate the timing of control methods and found results to be highly sensitive to changes in environmental and life history variables, especially mortality. A more complex individual based model incorporating daily changes in rainfall and temperature has been developed by Choi *et al.*¹⁴ temporal and spatial elements of slug dynamics, and includes stochastic effects in life expectancy and mortality. Growth was assumed to be logistic (based upon South³³); we derive a similar relationship from data in Sec. 2.1. Neither of these models elucidate the expected size distribution of the population, as opposed to the number of individuals.

In this paper, we initiate a systematic investigation into the relevance of size distribution on slug dynamics by modelling in a continuous fashion the size dependence of life history traits (individual slugs vary greatly in size (*D. reticulatum* typically grows from 10 mg to a mean of 922 mg, with some individuals reaching 2300 mg; for biological details see Begtsson and Baur⁹). Differences in size distribution may significantly effect the impact of a population on crops, as slug size is related to the capacity of the slug to consume food and disperse. Furthermore, most life history traits in terrestrial gastropods are directly related to body size, with the exception of the age at which slugs first reproduce.⁹ Here, we propose a nonlinear size structured model which incorporates effects due to a number of measures of the total population. For example, resource limitation is likely to be associated with potential food consumption by a range of slugs of different sizes and varying appetites. In this respect, total population biomass may be a more appropriate measure than the number of individuals feeding. In a similar vein, predation saturation may be expected to be dependent on the slug biomass within the predated range (see Sec. 2.3 below) of slug sizes.

Although slugs are prey to a large number of opportunistic species, in agricultural settings the principle predator is the carabid beetle *Pterostichus melanarius*;^{11,16,38} like all main predators of slugs, carabid beetles will readily switch to alternative food sources in their absence.²⁶ Although there is some weakly significant evidence to suggest that between-year beetle population growth is positively related to slug abundance,³⁸ it occurs over a long time scale and likely is mitigated by beetle migration. It is also not clear whether such a weakly significant correlation is simply the shared dependence upon a third factor, such as weather.

In light of such issues, we choose to incorporate beetle predation implicitly, since beetle population dynamics and their dependence on slugs are not sufficiently well understood to justify modelling populations separately, and this also allows for the inclusion of other similarly behaved predators, such as birds.

1.2. Brief overview of structured population models

Gurtin and MacCamy¹⁸ first proposed an age structured population model of the form

$$\begin{aligned} \frac{\partial s(t, a)}{\partial t} + \frac{\partial s(t, a)}{\partial a} &= -\lambda(P(t), a)s(t, a), \\ P(t) &= \int_0^\infty s(t, a) da, \\ s(t, 0) &= \int_0^\infty \beta(P(t), a)s(t, a) da, \end{aligned} \tag{1.1}$$

where the population density s is both a function of age a and time t , and the death rate λ and birth rate β are dependent on age and the total population P . Essentially, the first equation takes account of ageing and death processes, the second constructs a measure of the total population and the third models births (i.e. calculates the population at age zero). Existence and uniqueness of solutions was proven, and criteria for the existence and stability of steady age distributions ($s = s(a)$) derived. This model assumes that the “head count” P is the best measure of the effect of the total population on birth and death. However, for effects due to total food consumption, for example, we might expect older (larger) individuals to be more significant than younger (smaller) ones. Thus the governing equations (1.1) may be generalised by including a measure of the effect of the total population weighted by the density distribution.²⁰ In its simplest form, the population $P(t)$ is replaced by the integral

$$I(t) = \int_0^\infty w(a)s(t, a) da, \tag{1.2}$$

for some age-weighted function $w(a)$.

In addition to this, it is often more relevant to model the size of individuals (be it length or mass) rather than age. Linear models^{8,32} can admit analytical solutions in certain special cases (even for size and age structure³²). The nonlinear size-structured model of Murphy²⁵ essentially describes the same population dynamics as (1.1) but in terms of size:

$$\frac{\partial s(t, x)}{\partial t} + \frac{\partial g(P(t), x)s(t, x)}{\partial x} = -\lambda(P(t), x)s(t, x), \tag{1.3}$$

$$g(P(t), 0)s(t, 0) = \int_0^\infty \beta(P(t), x)s(t, x) dx, \tag{1.4}$$

where $g(P(t), x)$ is the growth rate of individuals of size x , and $P(t)$ is again the total number of individuals.

In this paper, we consider a more general size structured model where weightings are given both to the life functions of a species, to reflect the impact upon the population of different sized individuals, and to measures of the whole population (e.g. Metz and Diekmann²³). Thus an individual's development may depend upon

$$M_m(t) = \int_0^\infty m(x)s(t, x) dx, \quad (1.5)$$

where $m(x)$ is an appropriate weight function so that $M_m(t)$ is a weighted measure of the total population. If we define $m(x)$ as the mass of an individual of size x , then $M_x(t) = M_m(t)$ represents the population biomass at time t .

For slug populations the growth function g is unlikely to be strongly dependent upon the population number $P(t)$, or even $M_x(t)$. Any competition within the population is likely to be restricted to resource limitation resulting in starvation (and hence incorporated in the death rate) and, in laboratory experiments at least, growth is dominated by temperature.³³ Thus we may write $g = g(t, x)$, which allows for the inclusion of seasonal variations, although such variations are not considered in this paper. Furthermore, predators will respond to size-dependent sub-populations and so additional measures are required in the death rate.

The system becomes

$$\frac{\partial s(t, x)}{\partial t} + \frac{\partial g(t, x)s(t, x)}{\partial x} = -\lambda(M_x(t), M_p(t), x)s(t, x), \quad (1.6)$$

$$g(t, 0)s(t, 0) = \int_0^\infty \beta(M_x(t), x)s(t, x) dx, \quad (1.7)$$

where $s(t, x)$ is the density of individuals at time t of size x . In this model there is, in addition to a size dependence of life traits, an explicit dependence on the population's "size", and additional single or multiple dependences on measures $M_p(t)$, with the $p(x)$ yet to be specified. The inclusion of seasonal variations in environmental conditions (not considered here) would require further time dependence of life factors.

From a mathematical point of view, we have a nonlinear partial differential equation which has a functional dependence on nonlocal terms, with a nonlocal and nonlinear boundary condition with functional dependence on nonlocal terms. From a biological point of view the use of a structured model introduces the life history of each individual into the dynamics of the population, essentially due to the nonlinearities. Thus there exists feedback between the life history of the individuals and the whole population. The explicit details of the model are described in Sec. 2. Background for other size-structured population models, including existence and uniqueness theorems, can be found in recent publications^{15,20,23,39} (and references therein).

1.3. *Brief overview of current numerical methods with applications*

Often models such as those discussed above cannot be solved analytically and require numerical integration to obtain an approximation of the solution. In addition, the precise form of many of the life history functions of a population are often hard to determine, and the use of a numerical scheme may assist their construction by comparisons with field data. A number of numerical schemes exist, primarily for age- rather than size-structured models. Two main numerical approaches have been considered, the first of which is based upon standard difference schemes. These are used to approximate partial differential equations (upwind, box, Lax–Wendroff, Warming–Beam, method of lines, etc.), with adjustments to cope with nonlocal terms. The second, and most popular, approach is based upon integration along characteristic curves and seeks to solve the resulting coupled system of ordinary differential equations. Two categories of method have been considered: Runge–Kutta/multi-step methods; and the method for discretisation of a representation of the solution along characteristics. The review papers by Abia *et al.*^{1,2} compare the different numerical schemes with regard to accuracy, efficiency, generality, mathematical methodology and the qualitative behaviour subject to the compatibility conditions between initial and boundary data of the problems. The numerical methods employed in this paper are presented in the Appendix.

Modern numerical methods have been successfully applied to structured models to replicate available field and/or laboratory data, for a variety of different systems. Oscillations resulting from age-group specific nonlinearities in snail-host helminth populations have been considered,²² and experimental features reproduced in an age-structured population of blowflies³⁶ which indicated errors in previous, simpler, models. Stable equilibrium age distributions have been found in models by linearly interpolating time-dependent age-specific death and birth rates (e.g. Milner *et al.*²⁴). This has been extended by Angulo *et al.*⁷ with a more realistic model and a practical numerical method to accurately approximate the age density, with results that agree with data. Models with discontinuities have also been successfully studied numerically^{5,6} revealing the existence of bifurcations and providing approximations of stable solutions for both stationary and periodic populations. New properties of size-structured models with seasonal dependence (e.g. Sulsky³⁷) have been found through numerical simulation such as a global tendency to periodicity.⁴ These works indicate that structured population models and numerical simulations are new and exciting tools for investigating systems such as the one under consideration here.

2. Slug Population Model: *D. reticulatum*

In this section, we consider suitable functions, in the framework of (1.6) and (1.7), in order to model a size-distributed population of the slug *D. reticulatum*. In particular, we consider an agricultural setting, so that predation by carabid beetles will occur. The main components of the model are the growth rate g , death rate λ

and birth rate β . Here we shall set the slug size x to be mass, since this is the predominant factor which determines a slug's food consumption, egg production, susceptibility to predation, etc. We modify $m(x)$ such that

$$m(x) = \begin{cases} 0, & 0 \leq x < x_h, \\ x, & x_h \leq x \leq x_m, \end{cases} \tag{2.1}$$

where x_h is the size at which slugs hatch and x_m is the largest mass that slugs may attain, so that

$$M_x(t) = \int_{x_h}^{x_m} x s(t, x) dx \tag{2.2}$$

represents the total biomass of the slug population (excluding egg mass). This is the measure most likely to represent food consumption, which will have an impact upon the slugs through resource competition and influences crop damage. Here mass is in mg and time in days (d).

2.1. Growth rate

Before hatching, an egg has a negligible change in mass, whereas once the slug has emerged, it grows rapidly, slowing only as it becomes very large. Therefore, we naturally consider $g(x, t)$ in two parts.

During the egg stage, the time taken to reach the hatching size x_h is not dependent on size but determined by environmental conditions. In the absence of seasonal variations, we model the egg stage with constant growth ($0 \leq x \leq x_h$), based upon the average time (a_h) taken for an egg to hatch. An alternative formulation would be to include a time delay δ to represent egg development. The birth boundary condition (1.7) would then be imposed at the minimum hatched slug size ($x = x_h$), based on the egg production by individuals at time $t - \delta$. Here, the results would be identical, but such an implicit structure would make the inclusion of seasonal variations difficult in the future. In contrast, time dependence may easily be incorporated into the explicit growth rate (x_h/a_h above) to reflect, for example, the effect of cold weather on egg maturation.

In controlled conditions with regulated temperature slugs grow linearly at first before gradually approaching a maximum size.³³ We describe this age-mass relationship simply by

$$x(a) = \frac{x_m a}{\tau + a}, \tag{2.3}$$

where x_m is the maximum size attained and τ is the time taken for a slug to attain half this size. For constant $g_1 = x_m$, $g_2 = x_m \tau$ the growth function $g = g(x)$ is defined by

$$g(x) = \begin{cases} \frac{x_h}{a_h}, & 0 \leq x \leq x_h, \\ \frac{(x - g_1)^2}{g_2}, & x_h \leq x \leq x_m. \end{cases} \tag{2.4}$$

Continuity at x_h requires continuity of flux $g(x)s(t, x)$ —not necessarily $s(t, x)$ itself—which must be addressed by any numerical scheme used to simulate the problem (see Sec. 2.4 for discussion of the model and conditions at $x = 0, x_h$).

As discussed in Sec. 1, with seasonal variations such that $g = g(x, t)$ the growth (and hence size) is not determined by age alone. Explicitly, if $g_i = g_i(t)$ ($i = 1, 2$) then (2.3) would not be a solution of (2.4). It is to allow for such generalisation from the outset that we explicitly adopt a size-structured approach here.

2.2. Birth rate

Generally, slugs will not lay eggs until they have reached a certain mature size³⁵ x_l . *D. reticulatum* progress through three stages of development: immature juveniles, hermaphrodites acting as males and hermaphrodites acting as females. It is the larger slugs which usually function as females and lay eggs, and it is these forms which will determine x_l . However, an abundance of smaller slugs to act as males are not required, as larger slugs can take over this role as required, so fertile females will always be able to reproduce.

The timing of reproduction is also dependent on environmental conditions, since *D. reticulatum* can lay eggs opportunistically. In the absence of seasonal variations, however, egg laying is determined by size and previous reproductive behaviour alone.

Perhaps surprisingly, much larger slugs do not lay proportionally more eggs,³⁵ and in fact the number of eggs laid may reduce with x . This is partially due to the effects of illness and injury (age-related), but also because of the opportunistic laying behaviour of *D. reticulatum*. In ideal conditions, individuals' egg-laying rates reach a maximum some time after reaching maturity, with a gradual "exhaustion" induced decline.³³ Choi *et al.*¹⁴ assumed a weight-dependent egg production function fitted to a cosine curve over a fixed interval. We shall use a similar function with a well-defined peak at $x_e > x_l$, but shall insist that the function is continuous for all x and drops off sharply for large x (based upon observations in South³³). Hence, we set

$$\beta(x) = \begin{cases} 0, & 0 \leq x < x_l, \\ \beta_1 \frac{(x - x_l)}{(x_e - x_l)} e^{1 - \frac{(x - x_l)}{(x_e - x_l)}}, & x_l \leq x \leq x_m. \end{cases} \quad (2.5)$$

2.3. Death rate

We model slug death from three main sources: "natural" death, predation, and egg-laying cost. Each of these may be explicitly dependent on environmental conditions. In the absence of temperature and seasonal variations, dependence is restricted to both the size of an individual (due in part to age) and also the population as a whole.

Beetle predation is nontrivial but not well documented. However, experimental evidence does suggest that prey selection is a function of size, with very small slugs and very large slugs not preyed upon.¹⁶ If we let x_p be the slug mass most preferred by beetles then, consistent with the limited data,¹⁶ an appropriate smooth and normalised, prey selection function with compact support is

$$F(x) = \frac{1}{x_w} \cos^2 \left(\frac{\pi(x - x_p)}{2x_w} \right), \quad \text{for } |x - x_p| < x_w, \tag{2.6}$$

and 0 otherwise. Here $2x_w$ is the full width of the sinusoidal peak.

Beetles are opportunistic predators, moving into areas only if there is sufficient food; as a result predation levels are likely to be low when the slug population is small. It is unclear whether beetles respond to the total population in a region $I(t)$, based upon the number of slug encounters during a foraging expedition, or whether this is biased by the size of individuals encountered. Since beetles require a certain quantity of food for slug predation to be viable, it is more appropriate for this response to be proportional to the total biomass of slugs $M_x(t)$. In practice this may be mediated by size preference (see below) so that small and large individuals are not considered to be prey. It is thus reasonable to consider a predation weighted slug biomass measure, $\Pi(t)$, given by

$$\Pi(t) = M_{xF(x)}(t) = \int_{x_h}^{x_m} xF(x)s(t, x) dx, \tag{2.7}$$

weighted by the prey selection function, $F(x)$. Furthermore, for sufficiently large slug populations and finite numbers of beetles the predation rate is necessarily saturated. Hence, we assume a beetle response of the form

$$p_m \Pi^2(t) / (p_h^2 + \Pi^2(t)), \tag{2.8}$$

where p_m is the maximum predation rate, and p_h represents the *biomass* half-saturation level.²⁹

Later we shall also consider whether beetles respond instead to $M_x(t)$, the total slug biomass, rather than $\Pi(t)$. Such a scenario would be more appropriate if the beetles' predation response is due to chemical cues or slime trails.

We assume that the intrinsic death rate is independent of age, λ_1 , directly fitted to data.^{33,35} In addition to this, we introduce environmental limitation based upon total biomass, in the form $-M_x/K$, where K is some natural carrying capacity based upon a one hectare site, to represent resource competition. We assume that such an overcrowding effect is dependent on total population biomass, rather than number of individuals, purely reflecting the consumption of food, but this effect as with others may be adjusted if required.

The immediate death related cost of laying eggs may be written in a simple form as $\gamma\beta(x)$ for constant γ . Later we shall investigate this effect by fixing γ so that it doubles the natural death rate of the standard model at $x = x_e$. One might also investigate an *accumulative* egg laying cost, although this would add a further level of complexity and we do not consider this further here.

In summary, the total death rate for slugs (but not eggs) is given by

$$\lambda(M_x, \Pi, x) = \lambda_1 + \frac{M_x}{K} + F(x) \frac{p_m \Pi^2}{p_h^2 + \Pi^2} + \gamma \beta(x), \quad x_h \leq x. \tag{2.9}$$

There will also be a proportion of eggs which do not survive, assumed constant in the absence of seasonal variations:

$$\lambda(x) = \lambda_0, \quad 0 \leq x \leq x_h. \tag{2.10}$$

2.4. Structured model

The full structured model may be viewed from two equally valid and consistent perspectives. The system may be considered as composed of two coupled structured systems, for slugs and eggs, with “birth” conditions at both $x = 0$ (egg-laying) and $x = x_h$ (egg-hatching). Alternatively, the system may be presented as one mass structured system with a finite jump in s at $x = x_h$ due to the loss of continuity of g at x_h ; flux $g(x)s(t, x)$, however, is conserved. Mathematically, we require weak solutions to the equations in both egg and slug regimes and thus the eggs and slugs each have a value at $x = x_h$.

For convenience we choose the latter scheme and write the complete structured model for slugs based upon size as

$$\begin{aligned} \frac{\partial s(t, x)}{\partial t} + \frac{\partial g(x)s(t, x)}{\partial x} &= \begin{cases} -\lambda_0 s(t, x), & 0 \leq x \leq x_h, \\ -\left(\lambda_1 + \frac{M_x(t)}{K} + F(x) \frac{p_m \Pi^2(t)}{p_h^2 + \Pi^2(t)} \right) s(t, x), & x_h \leq x \leq x_m, \end{cases} \\ M_x(t) &= \int_{x_h}^{x_m} x s(t, x) dx, \quad \Pi(t) = \int_{x_h}^{x_m} x F(x) s(t, x) dx, \\ g(x) &= \begin{cases} \frac{x_h}{a_h}, & 0 \leq x \leq x_h, \\ \frac{(x - g_1)^2}{g_2}, & x_h \leq x \leq x_m, \end{cases} \end{aligned} \tag{2.11}$$

with quantities double defined at $x = x_h$, and boundary/compatibility conditions

$$s(t, 0) = \frac{a_h}{x_h} \int_{x_1}^{x_m} \beta(x) s(t, x) dx, \tag{2.12}$$

and

$$g(x_h^-)s(t, x_h^-) = g(x_h^+)s(t, x_h^+), \tag{2.13}$$

and $\beta(x)$ and $F(x)$ given by Eqs. (2.5) and (2.6), respectively.

3. Numerical Simulations

A detailed description of the numerical scheme is given in the Appendix, and is designed to be applicable beyond the specific model detailed in Sec. 2. The numerical scheme is implicit and is solved using fixed point iterations. The cost of implementation has been increased by the long timescale over which simulations are required to run, requiring excellent long term stability and convergence properties. For the simulations described herein, results of a large number of simulations over an extensive range of parameter values remain well-behaved and self-consistent.

3.1. *Parameter values*

We require $0 \leq x_h \leq x_l \leq x_m < \infty$ at all times, and $x_p \in [x_w, x_m - x_w]$ for predation. Parameter values have been estimated using laboratory³³ and field data^{12,19,34} where possible using standard fitting methods.²⁹ Laboratory data are taken for slugs in alternating conditions: at 10°C for 16 hours and 18°C for 8 hours, per day³³ (the most extensive source of data currently available). However, regular laboratory conditions such as these generally result in faster development than observed in the field. For example, slugs kept in favourable laboratory conditions produced eggs within 130 days of hatching,³³ whereas slugs in the field take up to twice as long in unfavourable conditions.^{19,33} Nonetheless, independently derived and consistent data are essential in order to properly assess the behaviour of the model.

For beetle predation on slugs, we have taken a number of values, within a realistic range employing the data of Digweed¹⁶ to calculate x_p and x_w , which display some of the possible effects upon the population distribution. The parameters for the *standard model* (SM) used in the simulations against which others are compared, are given in Table 1. In this paper, we present a number of representative simulations to illustrate the behaviour of the model, highlighting mechanisms associated with the modelling assumptions.

3.2. *Initial conditions*

Initial data for numerical simulations have to be chosen with care subject to compatibility conditions such that the data are consistent with the boundary conditions at $x = 0$ and x_h . We find that solutions evolving from a wide range of initial conditions are qualitatively similar for large time, including those initiated with uniform, egg-only, slug-only, and continuous multiple peaked size distributions. For the SM, initial data are assumed to consist of a single population of juveniles where neither eggs nor adults are present: $s(0, x) = 100$, for $20 \leq x \leq 50$, and 0 otherwise. Employing the advanced numerical methods described in the Appendix, these initial conditions evolve without numerical instabilities and naturally satisfy the compatibility conditions (2.12) and (2.13).

Table 1. Parameter values for numerical simulations of the model (2.11), (2.12) and (2.13). Here † indicates values obtained by fitting to data.

| Symbol | Description (with references) | Standard model | Other values |
|--------------|---|---|--|
| a_h | Mean egg hatching time ¹⁹ | 70 d | |
| x_h | Size of newly hatched slugs ³⁵ | 10.0 mg | |
| x_l | Maturation slug size ³³ | 425 mg | |
| x_m | Max slug size ³³ ($\equiv g_1$) [†] | 922 mg | |
| x_p | Preferred prey size ¹⁶ | 40.0 mg | 100; 450 |
| x_w | Half prey distribution width | 10.0 mg | 30; 90 |
| x_e | Slug size of peak egg production ^{33,†} | 445 mg | 500 |
| p_h | Level of half max predation | 0 mg | $(0.1; 0.5; 0.9) \times p_m$ |
| p_m | Max predation rate | $0 \text{ mg}^{-1} \text{ d}^{-1}$ | $(\frac{1}{10}; 1; 3) \times \Pi_{\max}$ |
| Π_{\max} | Max predation target | $\max_t \Pi(t)$ | |
| γ | Egg production cost | 0 d^{-1} | 0.00145 |
| K | Environmental carrying capacity ^{29,†} | $2.68 \times 10^8 \text{ mg d}$ | 2.68×10^6 or 10^{10} |
| g_2 | Growth constant ^{33,†} | $1.41 \times 10^5 \text{ mg}^{-1} \text{ d}$ | |
| β_1 | Max egg production rate ¹² | $1.40 \frac{\text{eggs}}{\text{slug}} \text{ d}^{-1}$ | |
| λ_0 | Egg death rate ^{35,†} | $1.52 \times 10^{-2} \text{ d}^{-1}$ | |
| λ_1 | Intrinsic slug death rate ^{13,33,35,†} | $1.45 \times 10^{-3} \text{ d}^{-1}$ | 0.0254; 1.45×10^{-4} |

3.3. Population evolution without predation

It can be shown^{23,27} that a unique steady state (given by the equilibrium value for the total biomass M_x) will always exist for the system (2.11)–(2.13), although it is difficult to determine its stability.²⁷ For the range of parameters investigated, numerical results indicate that the steady state is mostly stable, although the transient solution behaviour from arbitrary initial conditions may be observed over a very long timescale; solutions appear oscillatory with single or overlapping generations usually decaying to a stationary mass structure. Such asymptotic behaviour can be very sensitive to external forcing, and so may not be observed in the field; the transient behaviour may be the dominant feature of experimental data. In certain regions of parameter space oscillatory solutions appear globally attracting (see later).

We begin by setting parameters for the SM with values derived from experimental data, as above, but for the simplest scenario of no predation and no birth related death. Figure 1 shows the time evolution of the size distribution for one cycle of approximately 12,000 days. In the short term, the model naturally develops consecutive “generations” (in the absence of predation) that decay to a steady state mass structure, comparable with the Northfield field data presented in Choi *et al.*¹⁴ Figure 2 displays the total biomass of slugs with time, and it can be clearly seen that this reaches a steady state of approximately 4.7×10^6 mg. Each subsequent generation is formed once the current generation reaches maturity, and naturally extends over a greater range of masses as the mature slugs continue to lay eggs, albeit at a slower rate, until death. Such a population pattern forms for all initial conditions considered. From the final mass distribution we can calculate the

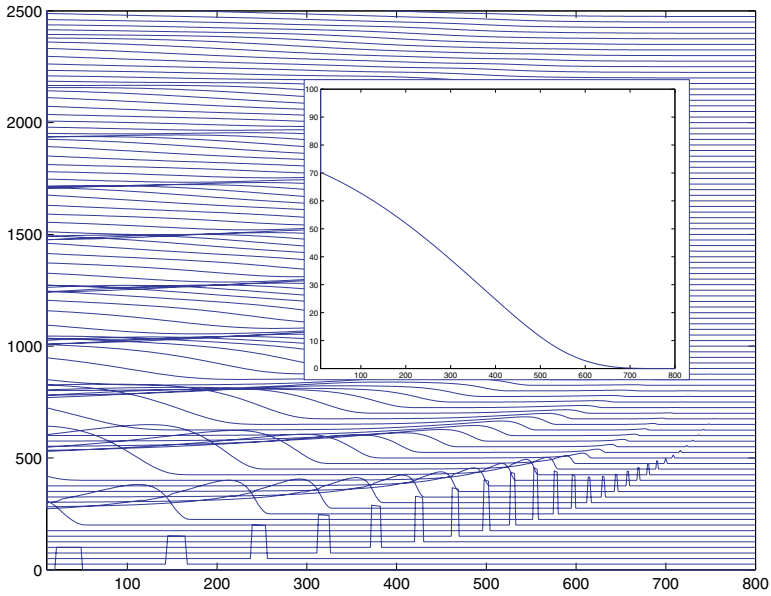


Fig. 1. The evolution of the size distribution (density in mg plus time in days) for the SM, showing the generational variations from a large number of small individuals to fewer large individuals, with a switch back to the original distribution as eggs are laid by older individuals that eventually die off. The pulses become broader and the solution tends towards a steady state size distribution, as depicted in the inset. Each line depicts the size distribution at intervals of 25 days, and the total time is 2500 days. (The numerical solution is computed at much smaller intervals; see the Appendix.)

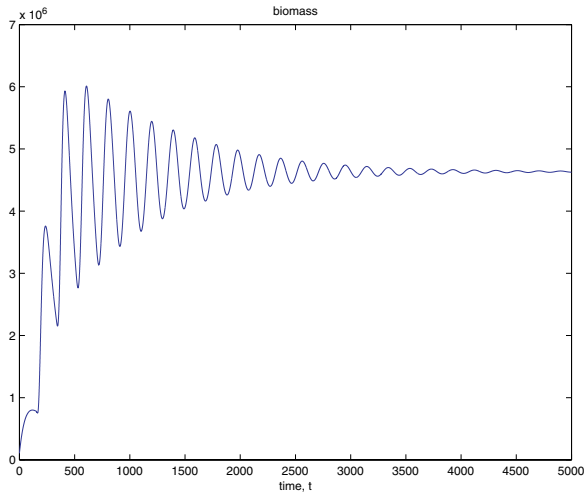


Fig. 2. The total biomass (mg) as a function of time (days) for the SM.

asymptotic proportion of adult (by which we mean mature egg-laying adult) to juvenile biomass:

$$\Gamma = \lim_{t \rightarrow \infty} \frac{\int_{x_l}^{x_m} xs(t, x) dx}{\int_{x_h}^{x_l} xs(t, x) dx}. \quad (3.1)$$

For the SM we find that this value is 0.2671, in line with the values that can be calculated from the Northfield field data.¹⁴

In what follows we systematically explore parameter space by varying the parameters in turn from those for the SM. Additionally we consider the terms that so far have not been considered.

Increasing the natural death rate λ_1 to 0.0254 d^{-1} , the value assumed in Choi *et al.*,¹³ leads to declining populations and finally extinction. Decreasing the SM value by an order of magnitude (setting λ_1 to $1.45 \times 10^{-4} \text{ d}^{-1}$) leads simply to larger populations, with little other variation. In both cases Γ remains unchanged. Dropping the value of the carrying capacity by a factor of 100 from the SM to $K = 2.68 \times 10^6 \text{ mg d}$ induces a similar drop in $s(t, x)$ throughout (again, Γ remains unchanged), and increasing to $K = 2.68 \times 10^{10} \text{ mg d}$ displays significantly larger population biomass ($\times 100$) and slightly longer generation times. Setting $K = \infty$ leads to unbounded solutions, suggesting that field populations do have an intrinsic environmental carrying capacity, as postulated in Sec. 2.

The birth kernel consists of a linear increase in egg production for $x_l \leq x$, followed by an exponential decrease (see Sec. 2.2). We can delay egg production and reduce the exponential decay considerably by moving the peak in the distribution of $\beta(x)$ (with $\max_x(\beta(x)) = \beta_1$) by increasing x_e from 445 mg to 500 mg. Of course, this also means that individual slugs will produce more eggs over their lifetimes, temporally extending the new pulse of eggs. The net effect is that generations are slightly delayed and populations slightly larger; the period of oscillations is 220 days compared to 200 days for the SM, the net biomass is approximately 15% greater, and the transients are much more quickly damped.

The additive birth related death term in essence models increased mortality due to the effort required to lay eggs. If we set γ equal to the value of the death term for the SM at x_e , then the birth-related death term will increase mortality around x_e subject to the distribution $\beta(x)$ so that it is double at $x = x_e$. Hence, we set $\gamma = 0.00145$, and find in this case that the birth-related death makes very little difference to generation time or net biomass. The long term size distribution changes marginally at the larger end of the size spectrum, but this change mostly occurs after the main egg production stage and has little effect upon the rest of the distribution. Thus we see that Γ is only slightly smaller at 0.2613.

3.4. Population evolution with predation

Predation is another aspect that we have so far overlooked. In what follows, we shall investigate first a standard predation model (SPM) and then we shall consider the

effect of adjusting the sigmoidal form of the predation function. Furthermore, we shall explore the overall strength of predation, the range of slugs considered prey and, finally, the form of the predator response. See Sec. 3.1 for a discussion of parameter values.

We start by defining the SPM by setting the preferred predation size x_p to be 40 mg and the half-width of the sinusoidal selection function $x_w = 10$ (see Sec. 2.3). Furthermore, we choose $p_m = \Pi_{\max}$, where Π_{\max} is the maximum value of the prey response measure $\Pi(t)$ for a predation-free run (i.e. for the SM). Finally, in order to explore the form of the predation function, we initially set the half-maximum predation level p_h by putting $p_h/\Pi_{\max} = p_h/p_m = 0.5$. Simulation indicates that initial pulse solutions become double peaked as they pass through predation vulnerable size classes and after the first generation the solution very rapidly tends towards a steady state size distribution with a maximum about 6 times less than for the predation-free SM, as in Fig. 3 with a total biomass of 7.2×10^5 mg, and an adult-juvenile biomass ratio Γ of 3.431. It is clear that for the SPM there is a much elongated and full tail for the steady state, and in stark contrast with the SM the distribution is not monotonic. This is due to a balance between the shape of the growth function, $g(x)$, the increased mortality of juveniles, and the resulting reduction in environmental carrying capacity induced mortality. We note that we have chosen parameter values to represent predators with voracious appetites, in order to highlight qualitative differences between the SM and the SPM regimes; it is likely that predation in the field may be less severe; simulations indicate lower values of Γ result when the effects of predation are reduced, although the non-monotonicity property is evident for low levels of predation.

Decreasing the ratio p_h/p_m to 0.1 we find that Γ is even larger at 6.909 and the tail is much more dominant. In other words, very large slugs dominate under conditions of selective juvenile predation. Increasing the ratio p_h/p_m to 0.9 has the effect of generating solutions somewhere between the SM and the SPM, with $\Gamma = 2.486$.

Continuing this theme, increasing the maximum predation rate (keeping p_h/p_m fixed) such that $p_m = 3\Pi_{\max}$ has the non-intuitive effect of increasing the final net biomass to 10^6 mg but shifting the local maximum of the size distribution to smaller slugs such that $\Gamma = 2.527$. This effect is due to the fact that in maintaining the p_h/p_m ratio we also increase p_h , which can reduce predation for levels of the predation target, $\Pi(t)$, below p_h . This is only partly tempered by increasing levels of the maximum predation level, p_m , and results in a shift of the population towards juveniles. Decreasing the maximum predation rate so that $p_m = \Pi_{\max}/10$ (p_h/p_m fixed) actually decreases the net biomass to 3.6×10^5 mg and increases Γ to 5.808. Reducing p_m to zero independently of p_h has the effect of removing predation, and the solution tends towards that of the SM.

Increasing the width of the prey selection function x_w to 30, the same as the width of the initial pulse, has the effect of damping the initial travelling pulse solution even quicker, but allowing sufficient slugs to survive to adulthood to generate

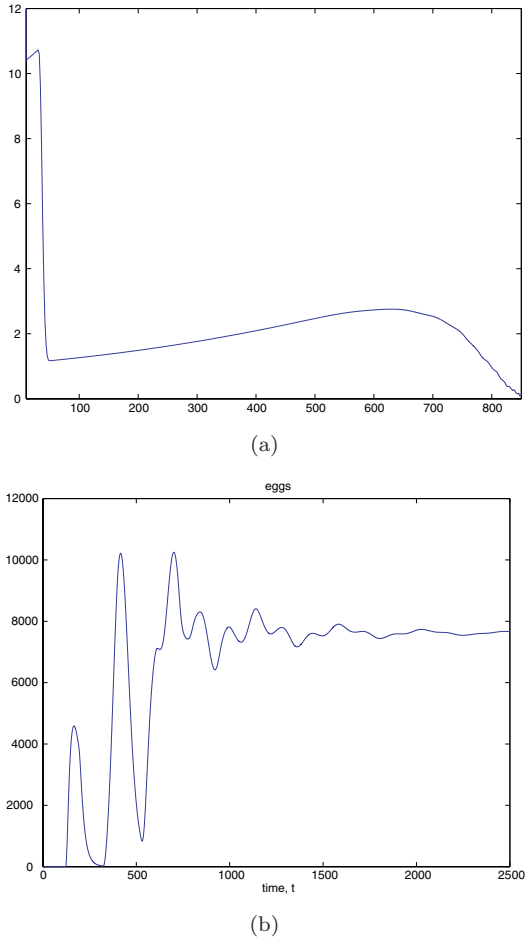


Fig. 3. The standard predation model (SPM). (a) Steady state size distribution. (b) Evolution of the number of eggs laid with time.

a steady state solution similar to the SPM, with $\Gamma = 3.291$, with some interesting transient behaviour that can be seen in Fig. 4 for the eggs laid (proportional to the birth biomass).

We may instead assume that the predators still select prey based upon their size, but are alerted to the slugs due to the whole population biomass (e.g. there may be chemical attractors) rather than the consumed biomass. Hence, we may consider replacing Π with M_x in (2.11). Simulations indicate that we get extinction as the relatively high beetle response strongly controls that population. Increasing the half-saturation parameter p_h to $2p_m$ allows the existence of a very small steady state population that possesses a maximum within the adult range, although no new behaviour was observed and transients generally die out quicker. Henceforth, we shall return to a beetle response of Π .

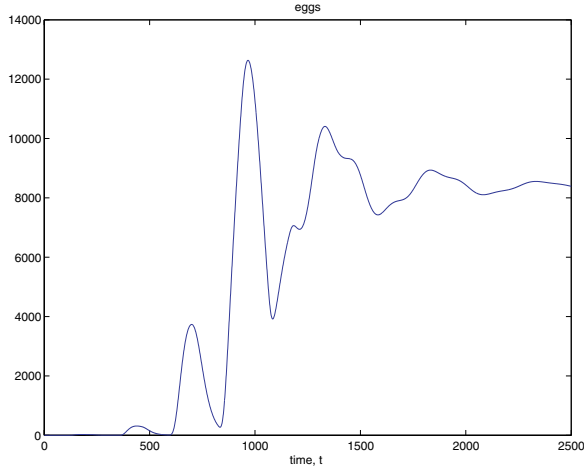


Fig. 4. The number of eggs laid as a function of time for the SPM with a wider prey selection function: $x_w = 30$.

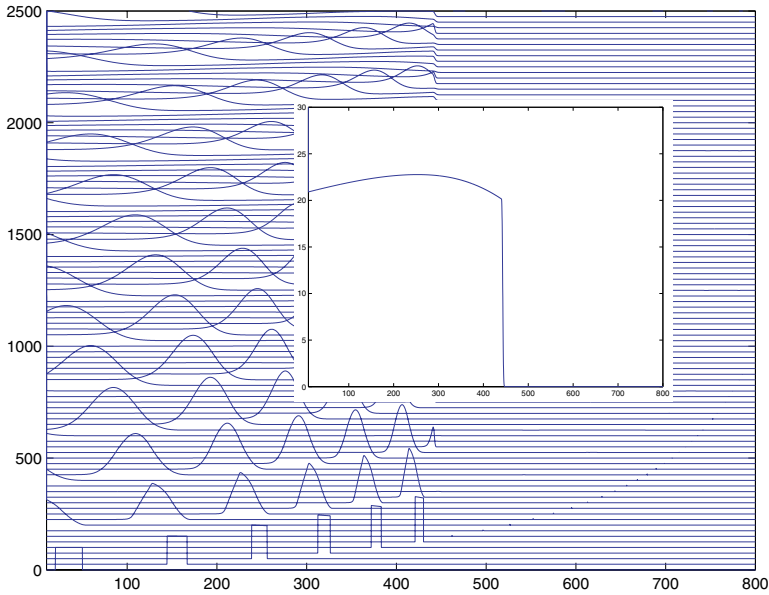
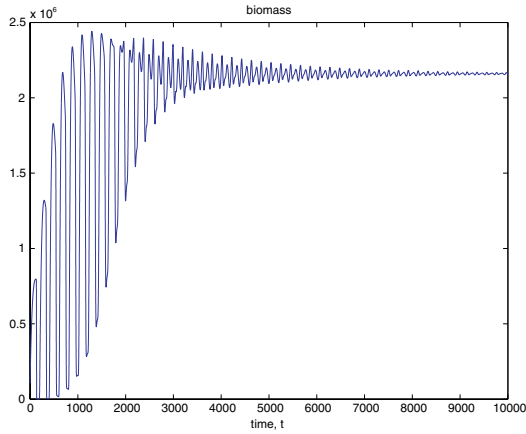
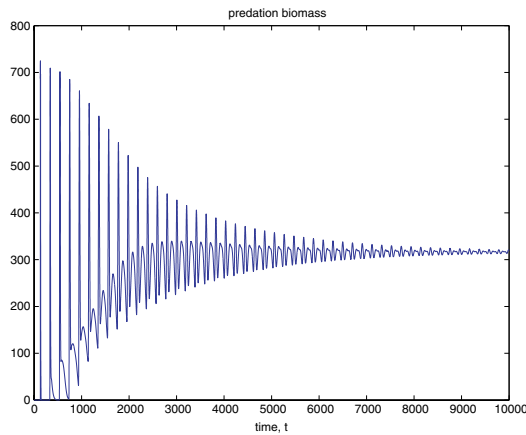


Fig. 5. The time evolution of the size distribution for the SPM with a very large preferred predation size of $x_p = 450$ mg. Mature egg-laying adults are rapidly predated, and the egg distribution adopts a pulse-like structure for a long period of time, associated with distinct generations. Eventually, however, the pulses become broader and the solution tends towards a steady state size distribution, as depicted in the inset. Each line depicts the size distribution at intervals of 25 days, and the total time is 2500 days. (The numerical solution is computed at much smaller intervals; see the Appendix.)

By increasing x_p such that $x_p = 450 \text{ mg} > x_l$ essentially we cap the slug population by removing larger slugs that in the SPM and SM are responsible for spreading the new generation of slugs over a wide range of sizes. Hence, we observe in Fig. 5 (for the evolution of the size distribution) and Fig. 6 (for the net biomass and biomass consumed by predators) the occurrence of oscillations in the form of distinct pulses, which can last for long times. This solution is a transient that over the course of many years converges to a steady state (as in the inset of Fig. 5; note that in Fig. 6 the predated population biomass appears to take longer to converge to a constant value due to the pulse-like nature of the solutions). The final value of Γ associated with this solution is 0.0805.



(a)



(b)

Fig. 6. (a) The net population biomass and (b) predated population biomass as a function of time for the SPM with $x_p = 450 \text{ mg}$.

With $x_p = 100$ and $x_w = 90$ we again quickly lose the travelling pulses and acquire a steady state, smoother than for the SPM, but with a net biomass of 4.1×10^5 mg and $\Gamma = 4.358$.

4. Conclusions

The inclusion of population size distribution measures is important in many models; for systems where there is a significant size dependence in life history factors, it is often necessary to consider size-weighted group feedback. In the slug model considered here, such weighted terms are biologically relevant in both resource limitation and predation saturation.

In this paper we have constructed a nonlinear size-structured model of slug dynamics that incorporates size specific aspects of natural death, resource limitation, predation, growth and egg production. We have been careful to base particular functional forms on experimental observation and data.

A major result of this work is the prediction of size distributions in non-predated and selectively-predated populations of slugs. It would be very interesting to compare these expected size distributions with field data subject to various environmental conditions. On this front, only limited field data is currently available.¹⁴ However, the shape of the predicted size distribution and the ratio, Γ , of adult to juvenile biomass in the non-predated model is consistent with these observations. Predators that only target slugs of particular size classes generally induce non-monotonic steady state distributions of slug biomass, and for juvenile predation give significantly larger values of the ratio Γ (an order of magnitude in this study). For large adult predation the value of Γ is significantly reduced. A clear-cut statistic such as Γ to implicitly determine the type of predation in the field could prove invaluable in agricultural settings.

Whilst most solutions eventually settle down to steady state solutions, the transient solutions are dominant for long periods (years) and any external noise or forcing is likely to excite oscillations and pulses (i.e. distinct generations). We clarify in this paper the regions of parameter space where oscillations are most likely. For example, for systems in which predators selectively predate large adult slugs, we find enticing evidence for long-term transient oscillations such that distinct generations of slugs persist, which suggests that the system with weak external forcing should provide a wide range of interesting solution behaviour.

There has been suggestion¹³ that physical forcing plays a significant role in the dynamics of slugs, although such conclusions were drawn from fitting an elementary model to a small set of non-independent data. A clear extension of the detailed model presented in this paper would be to include seasonal variations in environmental conditions (as investigated in detail in Schley and Bees²⁹). This would have the effect of removing the dependence of growth upon size alone. Growth, predation, birth and other terms would thus depend on time and size, e.g. reduced growth in cold weather and annual variations in beetle populations resulting in changes to

predation levels. We hypothesize that low frequency variations in the growth rate (seasonal changes) will induce the emergence of multiple peak distributions with overlapping generations. On the other hand, strong variations in egg maturation rates will help spread the population towards a single annual generation or steady state; it is expected that the strength of temporal variations will be significant in determining whether dynamics are dominated by single and multi-generational cycles, or the asymptotic behaviour of the system. It is likely that the transient and steady state solutions described in this paper will aid such an investigation. The development of a non-autonomous model of this form is a work in progress.

Appendix. Numerical Scheme

Simulations of the model (2.11)–(2.13) are made with a numerical method that integrates the equations along characteristic curves using a representation formula for the solution. The method takes into account the fact that the dynamics for slugs are more complex than the dynamics for eggs, and that slugs and eggs are related: new eggs depend on fertile slugs by means of a weighted integral, and new slugs are due to hatching eggs. To simulate eggs, we use a uniform grid and obtain the solution by means of an exact formula, except for eggs of minimum size which are calculated from a slug-dependent quadrature. For the evolution of slug numbers we employ a moving grid method with carefully selected nodes, following the ideas introduced in Ref. 3. This technique avoids potential accumulation of nodes close to the maximum size of the slugs (due to the form of the growth function) and increasing numbers of nodes at each time step due to newborns, but admits integration along characteristic curves. At each time level, we calculate the grid nodes and the approximation to the solution at these points by means of the characteristics method, except that slugs of minimum size are related to eggs of maximum size via continuity of flux. A theoretical integration along characteristics provides the next representation of the solution to the problem:

$$s(t, x(t; t_*, x_*)) = s(t_*, x_*) \exp \left(- \int_{t_*}^t \lambda^*(M_x(\tau), \Pi(\tau), x(\tau; t_*, x_*)) d\tau \right), \quad (\text{A.1})$$

where $\lambda^*(M_x(t), \Pi(t), x) = \lambda(M_x(t), \Pi(t), x) + g'(x)$, and $x(t; t_*, x_*)$ is the solution of

$$\begin{cases} \frac{dx}{dt} = g(x(t)), \\ x(t_*) = x_*. \end{cases} \quad (\text{A.2})$$

Given positive integers R and J and a fixed time interval $[0, T]$, we define $\Delta t = a_h/R$ (taking into account the form of the growth function), $\Delta x = (x_m - x_h)/J$ and

we set $N = [T/\Delta t]$. Thus, we introduce the $N + 1$ discrete time levels $t_n = n\Delta t$, $0 \leq n \leq N$. Next, we choose the initial grid nodes as $X_j^0 = j \frac{x_h}{a_h} \Delta t$, $0 \leq j \leq R$, and $X_{j+R}^0 = x_h + j\Delta x$, $1 \leq j \leq J$, and the numerical initial condition as the values of the theoretical initial condition at that nodes. As we consider separately eggs and slugs, we denote $L_j^0 = s(0, X_j^0)$, $0 \leq j \leq R$, and $U_j^0 = s(0, X_{j+R}^0)$, $0 \leq j \leq J$. We recall that the solution of our problem has a discontinuity (finite jump) at x_h , due to the form of the growth function, and the values $s(t, x_h^-)$ and $s(t, x_h^+)$ are related by $g(x_h^-)s(t, x_h^-) = g(x_h^+)s(t, x_h^+)$, $t \geq 0$. Thus, we understand that $L_R^0 = s(0, x_h^-)$ and $U_0^0 = s(0, x_h^+)$. In other words, x_h is a node of the grid and at each time level it will be associated with two values: one for eggs and the other for slugs.

Next, we present the first time level t_1 approximations. First, we compute the behaviour for eggs via the approximate integration

$$X_j^1 = j \frac{x_h}{a_h} \Delta t, \quad 0 \leq j \leq R,$$

$$L_{j+1}^1 = L_j^0 \exp(-\lambda_0 \Delta t), \quad 0 \leq j \leq R - 1.$$

Note that the grid is uniform with time due to the form of the growth function and that the value of L_0^1 is not obtained until we compute the values of the slugs at t_1 . Now, we compute the rest of the values of the grid and the solution for the slugs. They are computed by means of a second order method given by the following equations:

$$X_{j+R+1}^1 = X_{j+R}^0 + \Delta t g \left(X_{j+R}^0 + \frac{\Delta t}{2} g(X_{j+R}^0) \right), \quad 0 \leq j \leq J - 1, \tag{A.3}$$

$$X_{J+R+1}^1 = X_{J+R}^0 = x_m, \tag{A.4}$$

$$U_{j+1}^1 = U_j^0 \exp \left\{ -\Delta t \lambda^* \left(\frac{Q(\mathbf{X}^0, \gamma_{M_x}^0 \mathbf{U}^0) + Q(\mathbf{X}^1, \gamma_{M_x}^1 \mathbf{U}^1)}{2}, \right. \right.$$

$$\left. \left. \frac{Q(\mathbf{X}^0, \gamma_{II}^0 \mathbf{U}^0) + Q(\mathbf{X}^1, \gamma_{II}^1 \mathbf{U}^1)}{2}, X_{j+R}^0 + \frac{\Delta t}{2} g(X_{j+R}^0) \right) \right\},$$

$$0 \leq j \leq J - 1, \tag{A.5}$$

$$U_{J+1}^1 = U_J^0. \tag{A.6}$$

Finally, we compute the value of U_0^1 by means of the continuity of the flux

$$U_0^1 = \frac{x_h}{a_h} \frac{L_R^1}{g(x_h)},$$

and the incoming number of eggs by means of the discretisation of (2.11)

$$L_0^1 = \frac{a_h}{x_h} Q(\mathbf{X}^1, \beta^1 \mathbf{U}^1).$$

We have denoted $\beta_j^1 = \beta(X_{j+R}^1)$, $0 \leq j \leq J + 1$, $(\gamma_s^l)_j = \gamma_s(X_{j+R}^l)$, $0 \leq j \leq J + l$, $l = 0, 1$, $s = M_x, \Pi$; and

$$Q(\mathbf{X}^l, \mathbf{V}^l) = \sum_{j=0}^{J+l} q_j^l(\mathbf{X}^l) V_j^l, \quad l = 0, 1,$$

where $q_j^l(\mathbf{X}^l)$, $0 \leq j \leq J+l$, $l = 0, 1$, are the coefficients of the composite trapezoidal quadrature rules with nodes in \mathbf{X}^l . Also, $\gamma_s^l \mathbf{U}^l$, $l = 0, 1$, $s = M_x, \Pi$; and $\beta^1 \mathbf{U}^1$, represent the componentwise product of the corresponding vectors.

We observe that at consecutive times the number of nodes increases as a new node passes through x_h . Therefore, at the time level t_0 , we have $(R + J + 1)$ grid nodes and, at t_1 , we have $(R + J + 2)$. As discussed in Ref. 3, we may eliminate the first grid node X_{R+l}^1 that satisfies

$$|X_{R+l+1}^1 - X_{R+l-1}^1| = \min_{1 \leq j \leq J} |X_{R+j+1}^1 - X_{R+j-1}^1|. \tag{A.7}$$

Therefore, we keep fixed the number of nodes at the levels involved in the implementation of our step scheme: $(R + J + 2)$ nodes for the time level reached in the integration and $(R + J + 1)$ for the previous one. However, we do not recompute the approximations to the nonlocal terms at such time levels. Also, we have to note that the grid employed (subgrid of the complete one, in which all the nodes take part) is formed by x_h , the minimum slug size, together with the nodes obtained by integration along characteristics from the nodes selected at the previous time level.

Now, we describe the general time step, t_{n+1} , $0 \leq n \leq N - 1$. We suppose that the approximations and the grid at the previous time level t_n are known, then we define:

$$X_j^{n+1} = j \frac{x_h}{a_h} \Delta t, \quad 0 \leq j \leq R, \tag{A.8}$$

$$X_{R+j+1}^{n+1} = X_{j+R}^n + \Delta t g \left(X_{j+R}^n + \frac{\Delta t}{2} g(X_{j+R}^n) \right), \quad 0 \leq j \leq J - 1, \tag{A.9}$$

$$X_{J+R+1}^{n+1} = X_{J+R}^n, \tag{A.10}$$

$$L_{j+1}^{n+1} = L_j^n \exp(-\lambda_0 \Delta t), \quad 0 \leq j \leq R - 1, \tag{A.11}$$

$$U_{j+1}^{n+1} = U_j^n \exp \left\{ -\Delta t \lambda^* \left(\frac{Q(\mathbf{X}^n, \gamma_{M_x}^n \mathbf{U}^n) + Q(\mathbf{X}^{n+1}, \gamma_{M_x}^{n+1} \mathbf{U}^{n+1})}{2}, \right. \right. \\ \left. \left. \frac{Q(\mathbf{X}^n, \gamma_{\Pi}^n \mathbf{U}^n) + Q(\mathbf{X}^{n+1}, \gamma_{\Pi}^{n+1} \mathbf{U}^{n+1})}{2}, X_{j+R}^n + \frac{\Delta t}{2} g(X_{j+R}^n) \right) \right\}, \\ 0 \leq j \leq J - 1, \tag{A.12}$$

$$U_{J+1}^{n+1} = U_J^n. \tag{A.13}$$

Next, we compute

$$U_0^{n+1} = \frac{x_h L_R^{n+1}}{a_h g(x_h)} \tag{A.14}$$

and

$$L_0^{n+1} = \frac{a_h}{x_h} Q(\mathbf{X}^{n+1}, \beta^{n+1} \mathbf{U}^{n+1}). \tag{A.15}$$

We have denoted $\beta_j^n = \beta(X_{j+R}^n)$, $0 \leq j \leq J + 1$, $(\gamma_s)_j^n = \gamma_s(X_{j+R}^n)$, $0 \leq j \leq J + 1$, $s = M_x, \Pi$; and

$$Q(\mathbf{X}^l, \mathbf{V}^l) = \sum_{j=0}^{J+l} q_j^l(\mathbf{X}^l) V_j^l, \quad l = 0, 1,$$

where $q_j^l(\mathbf{X}^l)$, $0 \leq j \leq J+l$, $l = 0, 1$, are the coefficients of the composite trapezoidal quadrature rules with nodes in \mathbf{X}^l . Also, $\gamma_s^n \mathbf{U}^n$, $s = M_x, \Pi$; and $\beta^n \mathbf{U}^n$, represent the componentwise product of the corresponding vectors, $0 \leq n \leq N$.

Finally, we eliminate the first grid node X_{R+l}^{n+1} that satisfies

$$|X_{R+l+1}^{n+1} - X_{R+l-1}^{n+1}| = \min_{1 \leq j \leq J} |X_{R+j+1}^{n+1} - X_{R+j-1}^{n+1}|. \tag{A.16}$$

The solutions are defined by an implicit system of equations given by (A.12), which are solved by means of an iterative procedure.

The present scheme can be modified to treat problems where the growth function for slugs depends also on the whole population.

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