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Delay dynamics of the slug *Deroceras reticulatum*, an agricultural pest

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Abstract

Slugs are devastating agricultural and horticultural pests. However, their population dynamics are not well understood and this hinders the construction of efficient control strategies. This is especially true with organic farming for which biological controls are preferred. Moreover, the dominant species, *Deroceras reticulatum*, does not follow a regular annual life cycle, as do the majority of the other slug species. Its dominance may be associated with this fact. In this paper, we investigate whether mechanisms associated with the slugs' time-delayed population dynamics are responsible for the large variations in numbers, with particular emphasis on their sensitivity to environmental conditions. In order to do this, several versions of a non-autonomous delay differential equation model are developed in which we highlight some of the contentious issues in slug modelling. Analyses of the models are combined with numerical experiments using parameters based upon controlled laboratory experiments. In the absence of seasonal forcing, we find that the delay term may be neglected in the simplest models. However, the presence of a predator dramatically increases the impact of the delay term and may drive a delay induced instability. Notably, we find that in all cases the delay term is of considerable qualitative importance in models which incorporate seasonal fluctuations. We highlight the fact that the models are capable of producing a large range of solution behaviour and, furthermore, discuss the conditions for, and thus the likelihood of their relevance.

Keywords: Slug population; Biocontrol nonautonomous; Delay modelling

1. Introduction

Slugs are major pests in agriculture and horticulture, and are capable of causing widespread damage to seedlings, plants and crops. 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both in terms of biomass and numbers (Personal communication from D. Bohan, based on D.M. Glen, D. Bohan & co-workers, unpublished data: Long Ashton Research Station, IACR, UK, 2000). This species is a serious pest of global economic importance (South, 1992) as it has adapted well to the varied environments to which it has been introduced around the world (see for example Lovatt and Black, 1920; Quick, 1960; Dell, 1964; Altena and van Smith, 1975).

Chemical (methiocarb or metaldehyde pellets) are widely deployed as a means of control by both agriculturalists and horticulturalists. They may, however, have a number of drawbacks such as excessively

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degrading due to environmental conditions, causing pollution and being inapplicable to the increasingly popular practice of organic farming. In addition, common (carbamate-based) chemical treatments are indiscriminant, and kill other species including natural predators of slugs. There is evidence that the recovery time for "natural controls" such as carabid beetles is much longer than that of the target species, especially at critical times of the year (Purvis and Bannon, 1992; Purvis, 1996).

Recent work has indicated that treatments consisting of a parasitic nematode, *Phasmarhabditas hermaphrodita*, are effective against slugs (Wilson et al., 1993). These treatments are now available commercially to gardeners, but are currently too expensive to employ as alternatives to chemical treatments in conventional farming, even though they have been shown to be more effective if applied appropriately (Wilson et al., 1994).

It is desirable to maximise the effectiveness of these natural controls and to reduce or eliminate the need for chemical intervention. All nematode species are highly specialised and the presence of *P. hermaphrodita* does not affect any other organisms apart from slugs and snails (Glen and Wilson, 1997). To develop a treatment programme which maximises the reduction in slug numbers, and also reduces the cost of using nematodes in the agricultural setting, it is important to understand the temporal and spatial interactions of the nematode *P. hermaphrodita* with the slug *D. reticulatum*, and its environment (including other potential predators). A prerequisite for a successful biocontrol strategy is a full understanding of the dynamics of the slug *D. reticulatum*. This paper is concerned with the development and analysis of a reliable qualitative model of slug biomass. As a first step, we develop a number of (non-autonomous) delay differential equations (DDEs), and do not concern ourselves at this stage with spatial considerations. It should be noted that alternative model formulations have also been considered, such as a discrete-time model of egg production (Schley and Bees, 2002), and these provide similar results. Models of terrestrial gastropods differ from those developed for marine species (e.g. Coquillard et al., 2000).

Slugs are preyed upon by a large number of different species, including mammals, reptiles, birds and insects, although almost all predators readily switch to alternative food sources in the absence of slugs. In agricultural settings, the principle predators are the carabid beetles *Pterostichus melanarius* (Bohan et al., 2000; Digweed, 1993; Symondson et al., 2001). There is no evidence that *P. melanarius* is a specialist predator; it has been shown to consume a wide variety of prey (Sunderland, 1975; Pollett and Desender, 1986a,b). It is desirable to consider the effects of such predators, and whether they may prove to be a significant control in their own right (Asteraki, 1993; Ayre and Port, 1996; Chapman et al., 1997).

Recent work suggests that the number of beetles in the next generation may be affected by the current number of *D. reticulatum*, but that the effect of beetle numbers on the slug population is statistically less significant (Symondson et al., 2001). This weak dependence suggests that we might simplify the dynamics later in the paper for analytical convenience, although we still bear in mind the possible qualitative effects. Of greater significance to the models, however, will be the size of slugs that beetles predate (see below).

Of all the environmental variations that occur during the course of a year, temperature is considered to be the most important with regard to the life cycle of slugs (Wareing and Bailey, 1985; South, 1989a,b). Data are available (Hunter and Symmonds, 1971; South, 1982) linking slug growth and reproduction with temperature, and we make use of these data to construct the dynamics for an "average" year. Seasonal variation of the model parameters will thus be based on the changes in average monthly temperature.

The objectives of this paper are as follows:

- To develop simple single class models for slug population dynamics, based on the most significant life cycle factors.
- To give analytical predictions of populations in controlled environments, and the range of possible dynamics in variable environments.
- To study the effects of seasonal variation on slug populations, and give bounds on the expected population.
- To gain an understanding of the important factors and dynamics in slug populations, in order to develop simplified models to study biological control.

In Section 2 we discuss the model construction, and show how models may be employed for biomass or population number of either juvenile slugs, mature (egg laying) slugs, or the complete population. The benefits and suitability of each model are assessed in Section 2.1. The autonomous model is analysed in Section 3, giving results for controlled environments and indicating the possible behaviour in different regions of the parameter space. Non-autonomous parameters are constructed in Section 4, from laboratory data on *D. reticulatum*, and used in numerical simulations of the models. The results are discussed in Section 5.

2. Model construction

2.1. Quantifying slug populations

Although it may be more revealing to model slug population biomass, the following models are also applicable to the number of individuals. Biomass is used to allow for the large size distribution, since one may observe individuals ranging from 10 to 2300 mg. In addition, the mean individual size, and growth rate, varies throughout the year. Biomass may also be appropriate as a measure of crop damage, since the amount of food consumed will be dependent on the size of individuals (or, more strictly, mouth size). It should, however, be remembered that in commercial terms it requires only one slug to cause one item of produce to be unsalable. The number of individuals (rather than their total mass) may be more important with respect to interactions with other slugs or predators (as discussed later).

In this paper $S(t)$ will represent the slug population (either number of individuals or total biomass in mg) per m^2 at time t, measured in weeks. The definition of the variable S will in turn influence the scaling of the model parameters (to either count individuals or be related to mass): a full discussion is postponed until Section 4.1. If we wish to produce a model of slug numbers which still allows for size dependent characteristics, and quantifies individuals according to their size, we require a size structured model. Such a model for slug populations has been constructed (Schley et al., 2002), but the complexity of the system limits analytical progress and one must resort to numerical methods. An alternative approach is to break the population into a number of different class sizes, but this again adds complexity to the system and may not be justified at this stage.

In the interests of generality we describe in detail (in the following section), all the aforementioned combinations of model used in this investigation. In practice the data available will dictate which of the models will be used. We neglect spatial effects for the construction of these simple ("first step") models.

2.2. Reproduction

In the absence of migration, new members of the population are only added through reproduction by existing mature adults. We define adults as those slugs which are able to lay eggs (generally those above 200 mg for *D. reticulatum*). The life cycle of *D. reticulatum* includes a period during which young slugs have developed fully functional male reproductive organs, but have not yet become hermaphrodite. It is often found that these young slugs act as males while larger slugs take on the role of females. Since large slugs are hermaphrodite, however, the young slugs are not essential and their absence does not limit reproduction.

We represent the rate of viable egg production per unit of population which is capable of reproduction by $\rho \geq 0$. Here we define viable eggs as those which will hatch, usually only a small fraction of those laid (South, 1982). Since only a certain proportion of the population may be reproductively active, the egg production term $\rho(t)S(t)$ is required to be scaled by a measure of the proportion of the population that can lay eggs. The reproduction rate (with respect to time) is therefore modelled by $\tilde{\rho}(t)S(t)$, where we define $\tilde{\rho}$ explicitly below.

An important part of these dynamics however is the *time delay* between an egg being laid and the resulting slug being recruited to the appropriate population class. This delay, $\tau > 0$, may be a combination of the hatching time of the egg and the maturation time of the young slug (depending on the group being modelled), both of which are known to vary throughout the year. It has been shown (Tuljapurkar and Wiener, 2000) that reproductive delay and delayed development have the same effect on growth rate if they have equal costs (if the environmental pattern is time-reversible). We should not neglect this delay, since it may form a significant part of an individual's total life span. Any contribution to the current population through egg laying should be a function of the slug population (and egg production rate) at a time $\tau(t)$ ago. Thus, the increase in the population due to reproduction is given by

$$+\tilde{\rho}(t-\tau(t))S(t-\tau(t)). \tag{1}$$

2.2.1. *Class I: adult population model*

If $S(t)$ represents the adult population, then the delay τ between egg laying and recruitment is the sum of the hatching time t_{h} and the time taken for an individual to mature t_{m}. Both of these will vary considerably throughout the year (Hunter and Symmonds, 1971; South, 1982), largely due to temperature variation. We define $\epsilon_{\mathrm{s}}(t) \leq 1$ as the proportion of the viable eggs laid at time t which survive until adulthood. Reproduction then takes the form (1) by scaling ρ appropriately, i.e.

$$\tilde{\rho}(t-\tau) = \epsilon_{\mathrm{s}}(t-(t_{\mathrm{h}}+t_{\mathrm{m}}))\rho(t-(t_{\mathrm{h}}+t_{\mathrm{m}})).$$

2.2.2. *Class II: juvenile population model*

If $S(t)$ represents the juvenile population, then the delay between an egg being laid and an individual being recruited into this class is simply the hatching time: $\tau = t_{\mathrm{h}}$. We define $\epsilon_{\mathrm{m}}(t) \leq 1$ as the proportion of the total (combined) population which is mature, so that the egg producing (mature) population is given by $\epsilon_{\mathrm{m}}/(1-\epsilon_{\mathrm{m}})S(t)$. Scaled reproduction per unit of population is, therefore, of the form

$$\tilde{\rho}(t-\tau) = \frac{\epsilon_{\mathrm{m}}(t-t_{\mathrm{h}})}{1-\epsilon_{\mathrm{m}}(t-t_{\mathrm{h}})}\rho(t-t_{\mathrm{h}}).$$

2.2.3. *Class III: combined population model*

The proportion of the population which is mature is given by $\epsilon_{\mathrm{m}}(t)S(t)$, and $\tilde{\rho}$ is scaled accordingly. The delay is given by $\tau = t_{\mathrm{h}}$, since eggs are produced by (a proportion of) the current population and are immediately recruited into S upon hatching.

These expressions are summarised in Table 1. For a model of slug numbers, the parameter ρ simply represents the number of eggs produced by a mature individual. If $S(t)$ represents biomass, however, the number of eggs has to be scaled by the expected recruitment biomass per unit of producer biomass (see later).

In a similar way, the parameters ϵ_{s} and ϵ_{m} may either represent a fraction of the total number of individuals or a proportion of the total biomass.

Table 1
The different classes of model may all be accommodated by the full model (2.3) through rescaling of the parameters and variables denoted by the superscripts tilde (˜) or hat (ˆ)

Model class	Individuals modelled	Individuals predated	Variables ($\hat{S}$)	Parameters			
				τ	$\tilde{\rho}$	$\hat{a}$	$\hat{b}$
I							
i	Adults	None	–	$t_{\mathrm{h}}+t_{\mathrm{m}}$	$\epsilon_{\mathrm{s}}\rho$	–	–
ii		Juveniles	$S(t-\tau)$			ap	$b/\tilde{\rho}$[a]
iii		Adults	$S(t)$			a	b
II							
i	Juveniles	None	–	t_{h}	$\epsilon_{\mathrm{m}}\rho/(1-\epsilon_{\mathrm{m}})$	–	–
ii		Juveniles	$S(t)$			a	b
III							
i	Combined	None	–	t_{h}	$\epsilon_{\mathrm{m}}\rho$	–	–
ii		Juveniles	$S(t)$			a	$b/(1-\epsilon_{\mathrm{m}})$
iii		Adults	$S(t)$			a	b/ϵ_{m}
iv		Both	$S(t)$			a	b

Here the delays t_{h} and t_{m} represent the time taken from eggs being laid until individuals hatch, and from hatching until they reach egg laying size, respectively. The expected reproductive rate ρ for an individual slug must be scaled to take account of the class of individuals that is being modelled. Here, ϵ_{s} is the proportion of juveniles which have survived to adulthood, and ϵ_{m} is the proportion of the combined population which are mature individuals ($\epsilon_{\mathrm{s}}, \epsilon_{\mathrm{m}} \leq 1$).

[a] In this case we model the effect of predation on eventual recruitment, so that for the number of juveniles predated not to exceed those that are born we require $\hat{a} < 2\hat{b}$.

2.3. Population decay and limitation

We take natural death to be linear, so that the population is reduced by $d(t)S(t)$ per unit time, where $d \geq 0$. If we use biomass rather than number, the parameter $d(t)$ will need to be scaled accordingly, to take into account the size of removed individuals compared to average mass. In addition to this, biomass will increase due to the individual growth of slugs. Letting $g \geq 0$ represent the growth rate, and assuming the biomass increase is proportional to the actual biomass, we have a growth term of the form $g(t)S(t)$.

We define $\mu = d - g$ as the decay rate, so that the total rate of decrease in the population is given by

$$\mu(t)S(t).$$

Note that although it is possible that $g(t) > d(t)$ for part of the year, we would usually expect $\mu(t) > 0$, to counterbalance egg production, unless there exists some other limiting factor. In the case of modelling slugs with respect to number, $\mu = d$ (since $g = 0$), from which it immediately follows that $\mu > 0$.

In the case of the class II model of juveniles, there is the additional removal of individuals through maturation. For this model we assume that the mature proportion of the population is small, so that this departure term is negligible, since otherwise it is appropriate to use a different class model.

All environments have a “carrying capacity” (a maximum sustainable population due to finite resources), although it unlikely that slug populations ever reach this limit due to disease and parasitism at high densities (see South, 1992). It is thus pertinent to include a quadratic term in the model so that this limitation is only significant to the dynamics at high population levels:

$$\frac{-S^2(t)}{K(t)},$$

where $K(\tilde{\rho} - \mu) > 0$ is essentially the maximum sustainable population, irrespective of the limitation cause. Hence, we have implicitly assumed that all solutions remain bounded.

2.4. Predation

Carabid Beetles (*P. melanarius*) are the main predators of slugs in agriculture. Beetles predate slugs when they are in abundance, but can quickly turn to alternative sources of food if slugs are scarce. We thus consider their population and its effect implicitly, and assume a beetle predation term of the form

$$\frac{aS^2}{b^2 + S^2}, \tag{2}$$

where S is the population which is preyed upon. Here $a \geq 0$ represents predation saturation (i.e. the maximum quantity of slugs that can be consumed regardless of the actual quantity of prey available) and $b \geq 0$ is the population for which half this rate of predation is attained. This type of term results in little predation when prey numbers are low, which levels out to a maximum for high prey numbers. The probability that a beetle stays to predate in a region is determined by the probability of an encounter with a slug, which is clearly dependent on slug numbers. On the other hand, predation saturation is more closely associated with slug biomass, since predation activity is determined by how much total food a beetle has consumed, rather than the number of feeding encounters experienced. Since the current model does not take into account spatial encounters, medium population response and high level saturation, rather than the low level response, are the most important components to model accurately.

The most appropriate slug class to model is strongly influenced by which class are most predated. Bohan et al. (2000) found that *P. melanarius* attacked slugs above 25 mg, a lower bound which excludes only very early juveniles. Recent results (McKemey et al., 2001) suggest that this beetle will not attack slugs above 50 mg, although other species will (Pakarinen, 1994; Ayre and Port, 1996). This implies that mature adults (those above 200 mg) are not generally predated upon, although a large proportion of the juveniles are. If other predators (other carabids, birds, etc.) are included, however, then it is clear that larger individuals will also be removed. Birds in particular will often consume such prey opportunistically, with a preference for larger individuals.

The predation of different classes may be considered by modification of the predation term. Explicit rescalings of (2) are given in Table 1, and we outline their derivation here. Where appropriate we consider models with no predation (model subclass (i)) or predation of juveniles (ii), adults (iii) or both (iv).

2.4.1. *Class I*

For most of the models, predation is instantaneous (that is, the predation response at time t is a function of $S(t)$). This category clearly includes predation of adults (iii) in the adult population model. If, however, we consider a model of adults where it is the juveniles who are predated (ii), then the effect of predation on the population growth will be delayed. Predation will reduce the juvenile population which survive until maturity, and is thus a function of the zero-predated adult recruitment $\tilde{\rho}(t-\tau)S(t-\tau)$. The level of predation is proportional to the time juveniles spend being vulnerable to predation. We take p to represent this predation interval; for predation of *D. reticulatum* by *P. melanarius*, p is the time spent growing from 25 to 50 mg (Bohan et al., 2000; McKemey et al., 2001). Since this reflects a doubling in size, p may be approximated by manipulating the experimentally determined growth rate of individual slugs, g. Therefore, we set $p = \ln(2)/g$.

2.4.2. *Class II*

If the juvenile population is being considered, then juvenile predation (ii) is the only type of predation that it is suitable to incorporate. Otherwise it is more appropriate to model another population class.

2.4.3. *Class III*

The combined model easily allows for the predation of juveniles (ii), adults (iii) or both (iv), through a rescaling of a and b based on ϵ_{m} (the proportion of the population estimated to be mature).

2.5. *Governing equation*

We present the full generalised model:

$$\frac{\mathrm{d}S(t)}{\mathrm{d}t} = \tilde{\rho}(t-\tau(t))S(t-\tau(t)) - \mu(t)S(t) - \frac{S^2(t)}{K(t)} - \frac{\hat{a}(t)\hat{S}^2(t, t-\tau(t))}{\hat{b}^2(t) + \hat{S}^2(t, t-\tau(t))}, \qquad (3)$$

where the terms superscripted by a tilde (˜) or hat (^) are scaled appropriately, as summarised in Table 1.

3. Autonomous model analysis

The non-autonomous model is not amenable to non-numerical analysis, especially if we do not make assumptions about the behaviour of the parameters ρ and μ.

It is, however, still instructive to analyse the possible behaviours for fixed parameters, and thereby consider the distinct regions through which the model parameters may pass in time. In addition to this, there are certain situations in which agriculturalists have a highly controlled environment, such as a regulated greenhouse or polythene tunnel. Therein the effects of “rainfall”, humidity and (to some extent) temperature are kept relatively constant. Note also that in these environments we expect the predators to be dominated by beetles, but typically at a much lower level than in the field.

3.1. *Non-dimensionalisation*

When there is no time dependence of the *parameters* it is instructive to non-dimensionalise the model, to both simplify the analysis and the interpretation of results. Let

$$\bar{t} = \tilde{\rho}t,\ \bar{\tau} = \tilde{\rho}\tau,\ \bar{S}(\bar{t}) = \frac{S(\bar{t}/\tilde{\rho})}{\tilde{\rho}K} = \frac{S(t)}{\tilde{\rho}K},$$

$$\bar{\mu} = \frac{\mu}{\tilde{\rho}},\ \bar{a} = \frac{\hat{a}}{\tilde{\rho}K},\ \bar{b} = \frac{\hat{b}}{\tilde{\rho}K}.$$

Here $\bar{\rho}, \bar{K}, \bar{a}, \bar{b} > 0$, and since the decay rate $\bar{\mu}$ is independent of time we would also expect it to be positive, although our analysis is not restricted to this case. The model here is similar to the Spruce Budworm model (Ludwig et al., 1978), but with the inclusion of (multiple) delays. This produces a set of novel models whose dynamics are significantly different. Of particular interest is whether, in addition to the expected behaviour, we have a delay induced instability or limit cycle behaviour (not possible in the Spruce Budworm model). Substituting the above scalings, the non-dimensionalised autonomous model becomes

$$\frac{\mathrm{d}\bar{S}(\bar{t})}{\mathrm{d}\bar{t}} = \bar{S}(\bar{t}-\bar{\tau}) - \bar{\mu}\bar{S}(\bar{t}) - \bar{S}^2(\bar{t}) - \Pi(\bar{t}, \bar{t}-\bar{\tau}), \qquad (4)$$

where the predation term $\Pi(\bar t, \bar t - \bar\tau)$ is of the form

$$\frac{\bar a \bar S^2(\bar t)}{\bar b^2 + \bar S^2(\bar t)} \quad \text{or} \quad \frac{\bar a \bar S^2(\bar t - \bar\tau)}{\bar b^2 + \bar S^2(\bar t - \bar\tau)} \tag{5}$$

depending on the model class (see Table 1 for details).

The number and stability of possible steady states is dependent on the model class, and is also parameter dependent. In each case the steady state(s) $\bar S^*$ can be found by solving $\mathrm{d}\bar S^*/\mathrm{d}t = 0$.

3.2. *Time delayed dynamics*

Although the linear analysis of the steady states involves the delay τ, we may show (e.g. Schley and Gourley, 2000) that the delay will only affect (local) stability if there is a negative feedback in the delay. This only occurs in model class I (ii), where there is delayed predation; in all other cases it is sufficient to consider $\tau = 0$. The presence of a delay will, however, affect the global dynamics, such as the stability basins of steady states and the stability of non-steady solutions. This is particularly important when predation is included as both hysteresis and limit cycle behaviour may occur.

3.3. *In the absence of predation (Models I–III (i))*

Without delay or predation terms, the model reduces to the logistic equation. There exist either one or two steady states, namely $\bar S_0^* = 0$, and $\bar S_1^* = (1 - \bar\mu)$ if $1 > \bar\mu$. Linear stability analysis indicates that $\bar S_0^*$ is stable for $1 < \bar\mu$, and unstable when the inequality is reversed, in which case the positive steady state $\bar S_1^*$ exists, and is linearly stable.

3.4. *Unlimited resources with predation (Models I (ii and iii), II (ii), III (ii–iv))*

Neglecting the term representing the environmental carrying capacity constraint but including predation, the system has one or three non-negative steady states, given by $\bar S_0^* 0$ and

$$\bar S^*_{1,2} \frac{\bar a \mp \sqrt{\bar a^2 - 4\bar b^2 (1 - \bar\mu)^2}}{2(1 - \bar\mu)}. \tag{6}$$

Note that $\bar S^*_{1,2}$ are real and positive if and only if $\bar\mu \in (\bar\mu_c, 1)$, where

$$\bar\mu_c 1 - \frac{\bar a}{2\bar b}.$$

If $\bar a > 2\bar b$ then $\bar\mu_c < 0$ and $\bar S^*_{1,2}$ exist for all $\bar\mu \in (0, 1)$. We are usually only interested in positive values of $\bar\mu$ but the following analysis holds for all values. Note that when $\bar\mu = \bar\mu_c$, $\bar S_1^* = \bar S_2^* = \bar b$ for all $\bar a$.

For clarity in what follows we define

$$P_i^* = \frac{2\bar a \bar b^2 \bar S_i^*}{(\bar b^2 + (\bar S_i^*)^2)^2}.$$

Explicitly, $P_0^* = 0$ and

$$P^*_{1,2} = \frac{4(1 - \bar\mu)^3 \bar b^2}{\bar a^2 \mp \sqrt{\bar a^2 - 4(1 - \bar\mu)^2 \bar b^2}},$$

for $\bar\mu \in (\bar\mu_c, 1)$.

In the absence of delay, $\bar S_i^*$ is stable if and only if $1 - \bar\mu < P_i^*$. Conditions for stability when $\tau > 0$ will depend on the location of the delays. Section 3.2 indicates that a stability condition will only change if there is a negative feedback, i.e. $\hat{\bar S} = \bar S(\bar t - \bar\tau)$, and so we need to consider Case I (ii) separately.

3.4.1. *Positive feedback delay (Models I (iii), II (ii), III (ii–iv))*

Some analysis confirms what might be surmised graphically, that when positive steady states exist, the larger is always unstable and the smaller stable (see Table 2).

Note that there exists an explicit parameter range in which no steady state is (locally) stable. In addition, when a positive steady state does exist, its stability basin can be shown to be non-global, even in the absence of delay: the inclusion of a delay means that all stability results should be considered local unless proven otherwise. Predation may bound the population, but only if it is sufficiently strong ($\bar a$ sufficiently large with $\bar b$ sufficiently small). A prerequisite

Table 2
The existence and local stability of the possible steady states given by (6) as determined by the slug death rate $\bar\mu$

	Steady states
$\bar\mu < \bar\mu_c$	$\bar S_0^*$ (unstable)
$\bar\mu_c < \bar\mu < 1$	$\bar S_0^*$(unstable) $<$ $\bar S_1^*$(stable) $<$ $\bar S_2^*$(unstable)
$1 < \bar\mu$	$\bar S_0^*$ (stable)

for bounded solutions is the existence of $\bar{S}_2^*$, and this cannot occur when $\bar{\mu} < \bar{\mu}_c$, and so populations become unbounded. In such a case, a predation limited model is clearly inappropriate, and we must take into account other limiting factors which form part of the environmental constraints (see Section 3.5). The existence of a second positive equilibrium is necessary but not sufficient for bounded solutions. Moreover, in the absence of delay, we simply require the initial value of $\bar{S}(t)$ to be less than the threshold $\bar{S}_2^*$: the inclusion of delay means solutions are dependent on all previous $S(t)$, $t \in [-\bar{\tau}, 0]$ (see later).

3.4.2. *Mixed feedback delay (Model I (ii))*

We note that for the model to be consistent (i.e. the population born to be strictly larger than that consumed as juveniles) we require $\bar{a} < 2\bar{b}$ ($\bar{\mu}_c > 0$). In the absence of delay the results are as in Table 2. It can be shown that the steady state $\bar{S}_i^*$ will remain stable for all $\bar{\tau}$ if and only if $P_i^* < 1 + \bar{\mu}$. Since this condition is always met by S_0^* for $\bar{\mu} > 1$, and $\bar{S}_2^*$ is unstable whenever it exists, the equilibrium of interest is $\bar{S}_1^*$. Some algebra gives

$$P_1^* - (1 + \bar{\mu}) = \frac{1 - \bar{\mu}}{1 - \sqrt{1 - \delta}}\left((1 + \epsilon)\sqrt{1 - \delta} - (1 - \delta) - \epsilon\right),$$

where $\delta = 4(1 - \bar{\mu})^2\bar{b}^2/\bar{a}$ and $\epsilon = 1 + 2\bar{\mu}/(1 - \bar{\mu})$. By considering $\delta, \epsilon > 0$ the condition $P_1^* > 1 + \bar{\mu}$ can be shown to be true for sufficiently small positive $\bar{\mu}$.

The conditions which allow for the steady state S_1^* to bifurcate to instability for sufficiently large $\bar{\tau}$ are given by

$$P_1^* \frac{4(1 - \bar{\mu})^3\bar{b}^2}{\bar{a}^2 - \sqrt{\bar{a}^2 - 4(1 - \bar{\mu})^2\bar{b}^2}} > 1 \pm \bar{\mu} \quad \text{and} \quad \bar{\mu}_c < \bar{\mu} < 1, \tag{7}$$

which will be satisfied whenever $0 < 1 - \bar{a}/2\bar{b} < \bar{\mu} \ll 1$.

Explicitly, the solutions bifurcate when

$$\bar{\tau} = \frac{1}{\omega} \arccos\left(\frac{\bar{\mu}}{P_1^*}\right), \quad \text{where } \omega = \sqrt{1 - (\bar{\mu} + P_1^*)^2}. \tag{8}$$

Here ω is the frequency of the solution at the bifurcation point. The resulting solutions are oscillatory, as presented in Fig. 1. Note that, according to (8), the period of the bifurcating solution ($2\pi/\omega$) may be significantly different from the time delay ($\bar{\tau}$) present in the system which induced it.

Although the delay in the predation term may result in limit cycle behaviour that would otherwise not be present, it should be noted that the basin of attraction for these solutions turns out to be qualitatively similar to that of the equilibria solution $\bar{S}_1^*$ when it is stable. Thus, initial conditions which result in convergence to the equilibrium $\bar{S}_1^*$ when it is stable are likely to result in periodic (or quasi-periodic or even chaotic) solutions about the equilibrium when it is not.

While an undelayed system may have exact criteria for convergence to an equilibrium, and which may be easily expressed, the derivation of sharp conditions for the corresponding delayed system is unlikely to be possible in all but the simplest cases. Instead of the solution behaviour being determined simply by the starting value $s(0)$, all values of $s(t)$, $t \in [-\tau, 0]$ need to be considered as initial conditions. Suitable criteria for the solutions to converge to the equilibrium or to remain bounded are discussed in the Appendix A. The complexity of the stability basins is emphasised by the strong dependence of criteria not only on the initial values $s(t)$, $t \in [-\tau, 0]$, but also on the model parameters.

In the absence of delay a simple threshold on the initial value $s(0)$, namely $\bar{S}_2^*$, determines whether solution remain bounded or not. It may be shown (see Appendix A) that solutions of the delayed equation remain bounded if initial conditions $s(t)$ remain below this threshold for all $t \in [-\tau, 0]$. A rough rule of thumb is that initial conditions should remain below the threshold for a “sufficient” proportion of the delay time. What is sufficient however will again be strongly dependent on how much the initial conditions vary, and the model parameters. In the case of only small variations in $s(t)$, $t \in [-\tau, 0]$, it is the mean value of $s(t)$ on this interval which determines the solution behaviour (see Appendix A).

3.5. *Limited resources with predation (Models I–III (ii–iv))*

Such models are of the form

$$\frac{d\bar{S}(t)}{dt} = \bar{S}(t - \tau) - \bar{\mu}\bar{S}(t) - \bar{S}^2(t) - \frac{\bar{a}\bar{S}^2(t)}{\bar{b}^2 + \bar{S}^2(t)}. \tag{9}$$

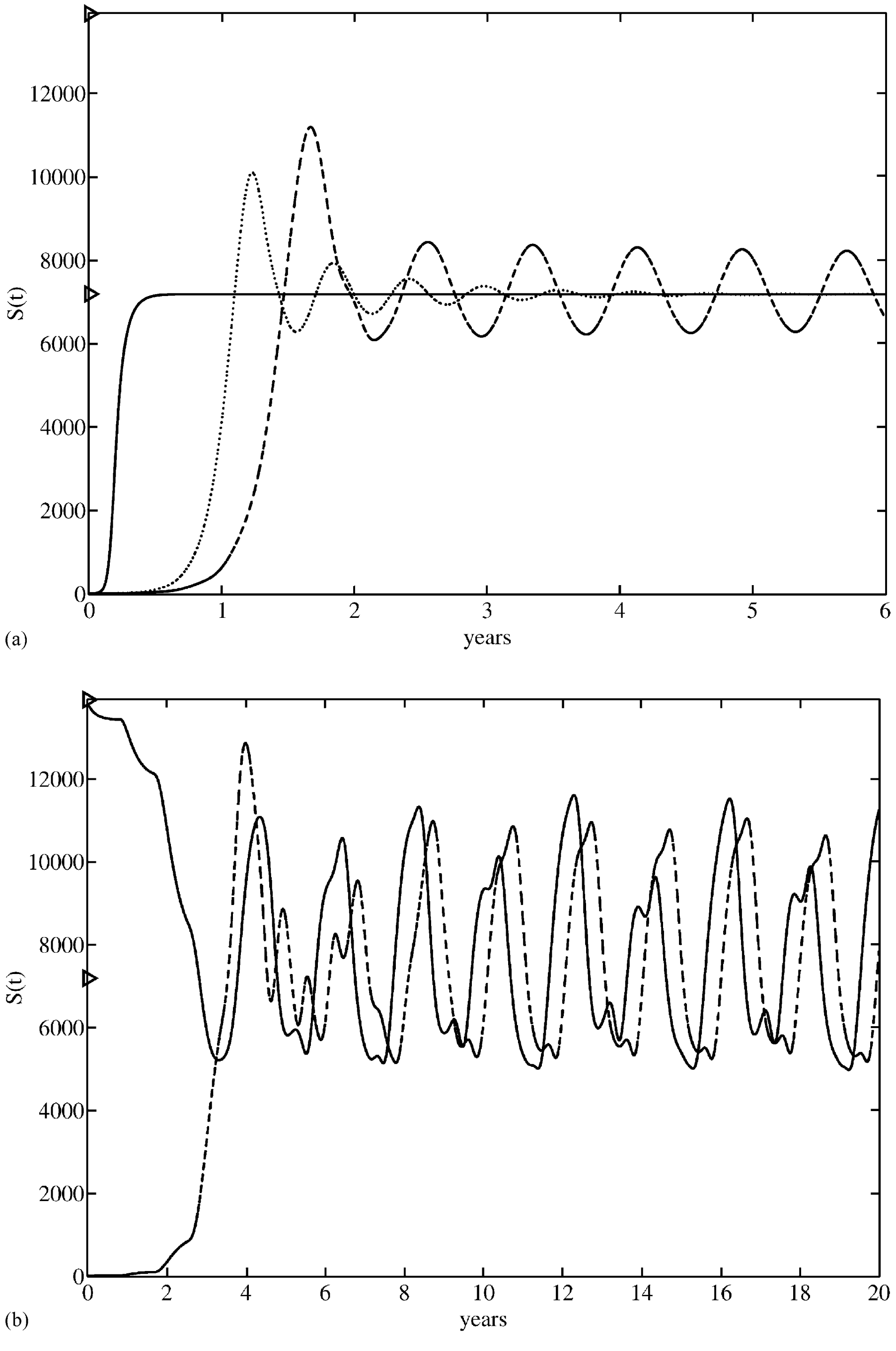

Fig. 1. An example of delay induced instability which can occur in the adult population when juveniles are predated (here $\rho = 1, p = 1, \mu = 0.1$ and $a = 1.9 \times 10^4, b = 1.0 \times 10^4$). (a) In the absence of delay the equilibrium $S_1^* = 7180$ is the only stable steady state, and attracts all solutions with initial conditions less than $S_2^* = 13{,}900$ (solid line). A small delay will not destabilise the equilibrium, but results in oscillatory, rather than monotone, convergence (dotted line; $\tau = 9$) for appropriate initial conditions. If the delay is sufficiently large ($> \tau_c = 13.4$), the steady state becomes unstable, so that there is no stable equilibrium solution and stable oscillatory solutions result (dashed line; $\tau = 14$). (b) Larger delays (e.g. $\tau = 43$) lead to what appear to be chaotic solutions, about the (unstable) steady solution S_1^*. All initial conditions which are less than S_2^* for a "sufficient" proportion of the time (see text) result in oscillations ($\tau > \tau_c$) or convergence to the equilibrium ($\tau < \tau_c$).

The steady states of (9) are given by $\bar{S} \equiv \bar{S}_0^* 0$ and the solutions of

$$-\bar{S}^* + (1 - \bar{\mu}) = \frac{\bar{a}\bar{S}^*}{\bar{b}^2 + \bar{S}^{*2}}. \tag{10}$$

By Descartes' Rule of Signs we may note that $\bar{S}_0^*$ is the unique steady state when $\bar{\mu} > 1$, but that otherwise there exists one or three positive roots of (10). For the rest of this section we shall assume $\bar{\mu} < 1$, since otherwise the dynamics are similar to the above. Bifurcation from one to three (or three to one) positive steady states (in addition to $\bar{S}_0^*$) will occur when the two curves, given by the left and right hand side of (10), touch tangentially. Defining

$$\bar{S}_{\pm}^* = \left(\frac{\bar{a}}{2} - \bar{b}^2 \pm \sqrt{(\bar{a}/2)^2 - 2\bar{a}\bar{b}^2}\right)^{1/2}$$

as the two possible double root steady states, this occurs when

$$\bar{\mu}_{\pm}(\bar{a}, \bar{b}) = 1 - \bar{S}_{\pm}^* - \frac{\bar{a}\bar{S}_{\pm}^*}{\bar{b}^2 + (\bar{S}_{\pm}^*)^2},$$

provided that $\bar{a} > 8\bar{b}^2$ (which implies that $\bar{\mu}_{\pm} < 1$). By considering when bifurcations with respect to $\bar{\mu}$ may occur (i.e. at $\bar{\mu}_-(\bar{a}, \bar{b})$ and $\bar{\mu}_+(\bar{a}, \bar{b})$), we subdivide the $(\bar{a}, \bar{b})$ parameter space into four main regions, as shown in Fig. 2. Only for a small range of values of $\bar{a}, \bar{b}, \bar{\mu} > 0$ we have the existence of three steady states, which in addition requires $\bar{\mu} \in (\bar{\mu}_-(\bar{a}, \bar{b}), \bar{\mu}_+(\bar{a}, \bar{b}))$. Conditions in which hysteresis due to the decay rate (bifurcation from one to three and then back to one steady state, with respect to positive $\bar{\mu}$) may occur, are even more restrictive. See Fig. 2 for details. Note that the vertical axis ($\bar{a} = 0$) is the case considered in Section 3.3.

3.5.1. *Positive feedback delay (Models I (iii), II (ii), III (ii–iv))*

If for each steady state we define Q^* by:

$$Q^* = 2\bar{S}^* + P^*,$$

then it can be shown that the steady state $\bar{S}^*$ is stable if $1 - \bar{\mu} < Q^*$, and unstable if the inequality is reversed.

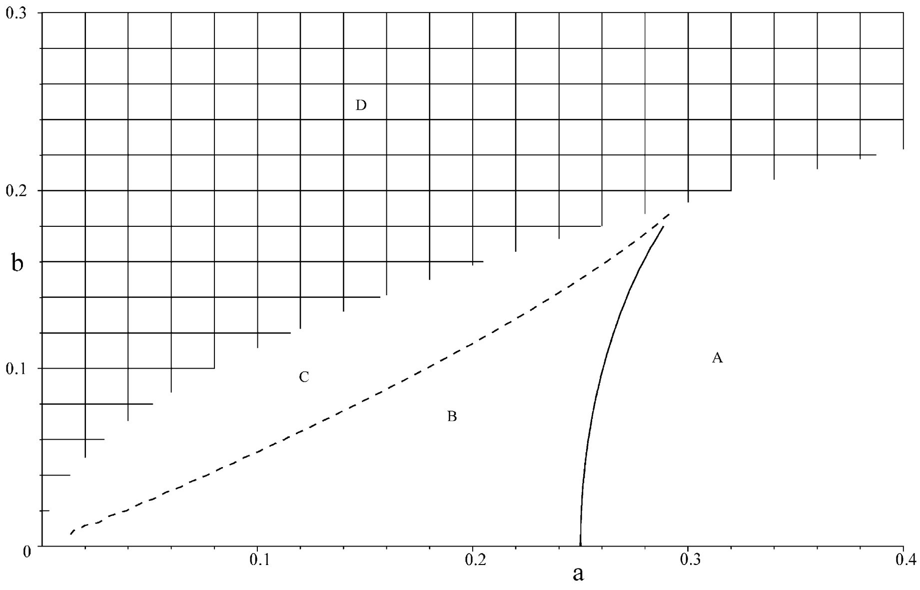

Fig. 2. The four main regions in the $(\bar{a}, \bar{b})$ parameter plane. In region A, we have one positive steady state for all $0 < \bar{\mu} < 1$ (where $\bar{\mu}$ is the decay rate), in addition to the zero steady state $\bar{S}_0^*$. In region B, three positive steady states are possible for sufficiently small (positive) $\bar{\mu}$, with one steady state for sufficiently large or small (negative) $\bar{\mu}$. In region C, we have three positive steady states for $\bar{\mu} \in (\bar{\mu}_-, \bar{\mu}_+)$, but only one otherwise. The solid line indicates the values of $(\bar{a}, \bar{b})$ when $\bar{\mu}_+ = 0$; for $\bar{\mu}_- = 0$ this is given by the dashed line. In all three cases we may switch from one to three to one steady state, although only in region C may this be achieved for non-negative $\bar{\mu}$. Region D is shaded to indicate $\bar{a} < 8\bar{b}^2$. In this region three positive steady states are not possible, and we again have only one positive steady state for all $\bar{\mu}$, in addition to $\bar{S}_0^* = 0$.

Note that $Q_0^* 2\bar{S}_0^* + P_0^* = 0$ so that $\bar{S}_0^*$ is always stable when the decay rate is larger than the birth rate.

For certain values of $\bar{a}$ and $\bar{b}$ we have bistability, and the initial conditions determine which stable steady state the solution converges to. Under such a regime, we have three positive steady states: the largest and smallest of which are locally stable, and the one in between is unstable. In the absence of a delay, solutions converge to either the larger or smaller steady state depending on whether $\bar{S}(0)$ is above or below the middle (unstable) steady state. When a delay is present such criteria are not sufficient, since initial conditions $\bar{S}(t)$, for all $t \in [-\bar{\tau}, 0]$, need to be considered (this is analogous to the resource unlimited case above). The consequences of this are discussed further in Section 4.7.

3.5.2. Mixed feedback delay (Model I (ii))

The analytical results for this model are rather long and thus have not been included here, but one can confirm what might be expected intuitively, namely that the addition of delay in the predation extends the above results to include the possibility of delay induced instability of equilibria, which may result in periodic or quasi-periodic solutions.

4. Non-autonomous seasonal model

In this section we consider possible forms and values for the non-autonomous parameters based on available data for the dynamics of *D. reticulatum* (under laboratory and field conditions). Furthermore, we shall perform numerical simulations of the model equations and assess the resultant solution behaviour. In general, we have not included differences between years, but have assumed that all parameters are periodic functions of time with period $T = 52$ weeks, giving a frequency of

$$\omega = \frac{2\pi}{T},$$

or a multiple thereof. This factors out the influence of inter-year variations, which we consider separately. Hereafter, S will be measured in either mg/m^2 or number/m^2, temperature, T, in °C and time, t, in weeks (wk), the later being the most natural unit to capture the annual fluctuations.

4.1. Parameter estimation

4.1.1. Reproductive delay

As previously discussed, the delay $\tau(t)$ is not only of a large magnitude, but also varies throughout the year. Depending on the class of model being considered, this time lag may consist of the hatching time of eggs (t_h), or the time taken for juveniles to mature (t_m), or a combination thereof (see Table 1). Hunter and Symmonds (1971) recorded the number of weeks to hatching for outdoor eggs, showing a variation between 4 and 14 weeks. The time taken to mature is based on an estimate (using South, 1982) of 2600 day degrees required for a hatchling to become a mature egg laying adult. By considering the average temperature for each month of the year (National Climate Data Centre, 2000), we have evaluated the time taken to accumulate these day degrees. The calculated values are plotted in Fig. 3.

The parameter $\tau(t)$ represents the delay time *since laid* of a slug which has hatched, or attained maturity, at time t. The two relevant curves t_h and $t_h + t_m$ are conveniently fitted by

$$\begin{aligned} \tau(t) &= t_h = 7.08 + 4.59\sin(\omega t - 4.99) \\ &\quad + 1.75\sin(2\omega t - 5.02)\ \text{week}, \qquad (11) \\ \tau(t) &= t_h + t_m = 43.2 + 3.93\sin(\omega t - 2.05)\ \text{week}. \end{aligned}$$

4.1.2. Temperature dependent rates

All other parameters were estimated through a two stage process based on the temperature dependent life cycle data of South (1982) and the average monthly temperature in Britain (National Climate Data Centre, 2000). Temperature is the most important external factor determining slug dynamics (Wareing and Bailey, 1985; South, 1989a,b), especially since it influences other factors such as soil moisture. Here we consider results under laboratory conditions, since this provides a more reliable response to temperature. *D. reticulatum* has also been studied in permanent pasture (South, 1989a), which provides some limited data, although it is subject to an assortment of environmental variations. The effects of changing temperatures appear most significant in the context of activity and development (Wareing and Bailey, 1985).

Data points were generated by employing the observed development and breeding behaviour of *D. reticulatum* at constant temperature. Results are,

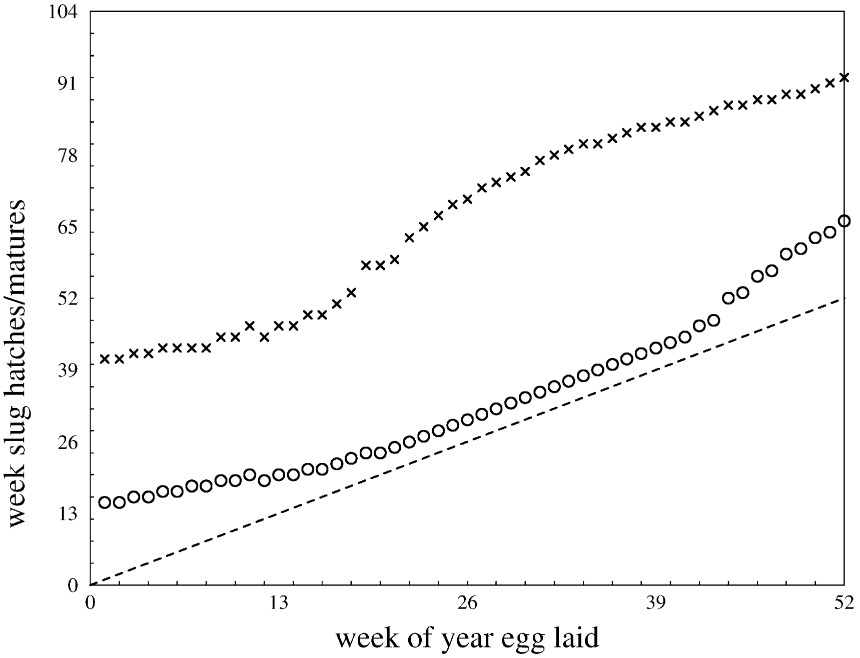

Fig. 3. A plot of the week of the year (or next year, for weeks >52), in which slugs hatch (○) and become reproductively mature (×) against the week of the year in which eggs are laid. The value of the delay t_h for each week of the year is the interval between the current time (dashed line) and hatching time ○, whilst t_m is the interval between the hatching time ○ and maturing time ×.

therefore, based on a limited, but biologically consistent, number of points. A margin of 1 standard error (S.E.) was included for each set of laboratory data used. Since this does not allow for the expected correlation between, for example, mass and lifespan, this is a conservative upper bound on the true S.E.

Definitions of the temperature dependent parameters $\rho(T)$, $\mathrm{d}(T)$ and $g(T)$ (representing egg production, death and growth, respectively) are given in Table 3. Adapting the parameters for a biomass model (as opposed to a model of slug numbers) requires a rescaling, based on the size of individuals at significant life events, but in each case the units are expressed in week^{-1}.

Piecewise functions $\rho(T)$, $\mathrm{d}(T)$ and $g(T)$ were fitted to the mean, upper bound and lower bound of the data, giving three temperature dependent (piecewise linear) curves in each case. Thus, by considering the average (monthly) temperature throughout the year $T(t)$, data was generated for the the growth, death and egg production rate as functions of time. Curves of the form

$$\alpha_1 + \alpha_2 \sin(\omega t + \alpha_3) + \alpha_4 \sin(2\omega t + \alpha_5)\ (\geq 0\,\forall\, t), \tag{12}$$

were fitted for $g(t)$, $d(t)$ and $\rho(t)$, for the three possible cases (piecewise mean, piecewise minimum and piecewise maximum). The functional form (13) reflects the annual periodicity of the parameters, and also their experimentally observed behaviour with a single or double maxima distribution over the year.

The fitted data for mature (model class I) biomass is thus given by

$$\begin{aligned} \rho(t) &= (25.27 - 5.62\sin(\omega t + 7.46) \\ &\quad + 1.68\sin(2\omega t + 4.04)) \times 10^{-2}\,\mathrm{week}^{-1}, \\ d(t) &= (20.54 + 8.97\sin(\omega t + 4.30) \\ &\quad + 1.15\sin(2\omega t + 4.96)) \times 10^{-3}\,\mathrm{week}^{-1}, \\ g(t) &= (19.06 + 1.28\sin(\omega t + 4.51) \\ &\quad + 6.27\sin(2\omega t + 4.11)) \times 10^{-3}\,\mathrm{week}^{-1}. \end{aligned} \tag{13}$$

Table 3
Derivation of the egg production (or recruit biomass) rate ρ, the death rate d and growth rate g, as determined by the available temperature dependent laboratory data (South, 1982)[a]

Class[b]	Individual model	Biomass model scaling
ρ		
I	Number of viable eggs[c]/mature lifetime	Mature recruit mass/average mature mass
II		Hatchling mass/average mature mass
III		Hatchling mass/average mature mass
d		
I	1/total lifespan	Maximum mass/average mature mass
II		Maximum mass/average juvenile mass
III		Maximum mass/average juvenile mass
g		
I	–	Mature mass increase/(mature lifetime)(average mature mass)
II		Juvenile mass increase/(immature lifetime)(average juvenile mass)
III		Juvenile mass increase/(immature lifetime)(average juvenile mass)

[a] In each case the parameter for the individual based model is scaled (by a mass ratio) to give the biomass model parameter. Note that for both models, all the parameters have the required units of week^{-1}.

[b] For model classes, see Table 1.

[c] Only a small proportion of the eggs laid (South, 1982) actually hatch (South, 1992).

Initially ρ is of a different order of magnitude to d and g (further exacerbated by the fact that $\mu = d - g$). The significant parameter, however, is the ratio between μ and the scaled parameter $\tilde{\rho}$ (see Section 2.2). The parameters (13) also agree with the limited field data: see South (1989a) for estimates of the growth rate of slugs, and Carrick (1938) for egg production of *D. reticulatum*.

4.2. Modelling parameters

The parameter K, derived from the carrying capacity, will be dependent on the particular environment and, to a lesser extent, on the specific environmental conditions of any given year. We note, however, that unfavourable homogeneous habitats are equivalent to smaller more favourable ones. When considering slugs in isolation, solutions remain qualitatively identical irrespective of K (i.e. scaling K scales the solution). This is not true in the presence of predation, as the definitions of parameters a and b depend explicitly on the quantity of predators. Unfortunately, there are no suitable data available for giving a quantitative measure of beetle predation on slugs (see later for estimates).

Since populations of up to at least 400 slugs/m^2 have been recorded, we consider a carrying capacity of at least that number. In the case of biomass, we assume that the maximum population per square meter consists of 400 small juveniles (approx. 25 mg), which would be equivalent to the presence of just four maximum sized mature individuals (approx. 2300 mg for *D. reticulatum*). In the absence of suitable data, the carrying capacity (given at any instant by $K(\tilde{\rho} - \mu)$) is taken as constant.

The choice of model class can be based upon the reliability of the estimates for ϵ_s and ϵ_m. In what follows we derive an estimate for ϵ_s, and thus consider the model for mature slugs (class I). In particular, ϵ_s is subject to less temporal variation, and may be derived through the use of a subset of the information required for other models.

The scaling $\epsilon_s(t)$ represents an estimate of the proportion of juveniles laid at time t which survive to adulthood. If we assume that individuals of a certain age class (and size) only compete with each other for resources, then the number of juveniles J hatched at $t = 0$ which survive until time t is determined by

$$\frac{dJ}{dt} = -\mu J - \frac{J^2}{k},$$

where k is natural carrying capacity of the juveniles. Solving for J (for constant parameters) we have

$$J(t) = \frac{dk\,J(0)e^{-\mu t}}{\mu k + J(0)(1 - e^{-\mu t})},$$

so that the proportion surviving a time τ to maturity is given by

$$\frac{e^{-\mu\tau}}{2-e^{\mu\tau}}, \tag{14}$$

where we take the natural carrying capacity of the group as the total number of hatchlings initially born, giving $k = J(0)/\mu$. If we neglect the carrying capacity in the above (and so assume that juveniles do not face overcrowding competition) then the proportion which attain maturity is instead simply given by

$$e^{-\mu\tau}. \tag{15}$$

We take (15) as an upper bound on the estimate (14) of the parameter $\epsilon_S(t)$.

Hence, the mean value of $\epsilon_S(t)$ (using the mean of the *juvenile* death rate $\mu = d$ and the maturation delay $\tau = t_m$, see Table 3) is

$$\epsilon_S = 5.37 \times 10^{-2}, \tag{16}$$

with an upper bound of 1.01×10^{-1}. Temporal variation in $\epsilon_S(t)$ is incorporated by inclusion of a time dependent delay, as determined by (11). Note that now $\tilde{\rho} = \epsilon_S\rho$ is of comparable magnitude to $\mu = d - g$.

For class I biomass models (parameters given by Eqs. (13) and (16)) we have

$$K = 1.41 \times 10^6\ \text{mg week}. \tag{17}$$

4.3. Model type

Numerical investigations of the model suggest that models of both biomass and population number give qualitatively similar results. However, Bengtsson and Baur (1993) found that all life history traits in terrestrial gastropods were related to body size, with the exception of the age at which slugs first reproduce. It is, therefore, perhaps more appropriate to model slug biomass.

The number of individuals is of greater importance when we consider individual interactions (including responses to overcrowding and slime-trails), but in this paper we do not include spatial dynamics and thus these issues are less relevant. Predator response may be influenced by the number of prey present, but this will be most significant at low predator/prey numbers or across large spatial scales. For the spatially uniform population model, however, it is more important to accurately model predation saturation, which will be a measure of the total mass of slugs, rather than the number of individuals. The inclusion of slug growth, which varies considerably through the year (e.g. (13)) also lets us consider the difference in slug feeding activity (see Section 4.6). In the simulations below, we thus consider $S(t)$ as a measure of slug biomass, and modify the parameters accordingly (see Table 3).

4.4. Population dynamics

Some examples of stable periodic numerical solutions are shown in Fig. 4. Solutions for the upper and lower bounds (obtained when fitting the temperature dependent experimental data to 1 S.E.) have been presented in order to demonstrate the range of solutions that are possible (such as extinction) by varying the model parameters. However, we would expect that a particular species of slug would have only one such response to temperature, unless additionally affected by external factors. The natural period of 52 weeks observed in Fig. 4 is a result of the forcing functions, d, g and ρ. In essence, the dynamics are entrained by the pseudo-steady equilibrium $\rho(t-\tau(t))-\mu(t)$, which may be negative for part of the year, and the time delays have the effect of introducing oscillatory transient solutions. Thus, the effect on the long-term solution in Fig. 4 appears limited. When considering the forcing functions it should be remembered that the presence of a *variable* delay means that $\rho(t-\tau)$ is qualitatively different to $\rho(t)$.

Slug distributions over the course of the year generically show two peaks, indicating spring and autumn increases. This is a result of both favourable conditions and the variable delay.

4.5. Annual variation

The results in Section 4.4 are based on the monthly UK temperatures, averaged over a 30-year period. Thus, we have generated what might be considered as an "average" population. These average monthly temperatures do, however, neglect the large variation in temperature between years; certain years may be significantly warmer or cooler than others. At this stage, we have not considered simulations with constantly varying temperatures across several years as we feel that it would obscure recognition and analysis of the

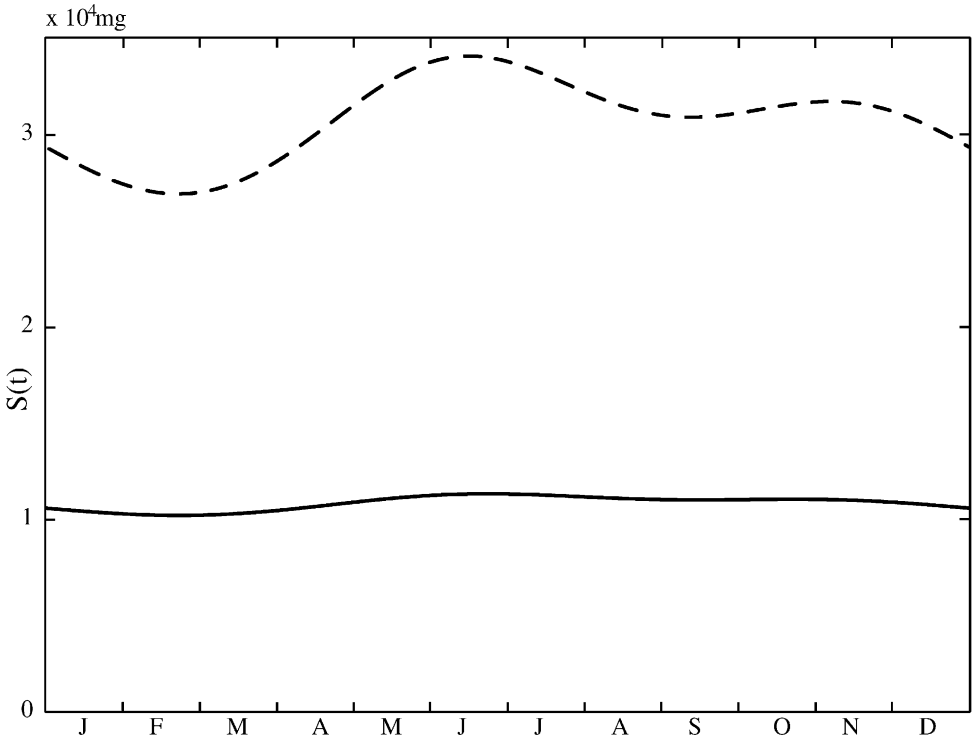

Fig. 4. If the conditions are the same each year, the population biomass fluctuates periodically (with a period of 1 year). Simulation results for the parameters calculated by piecewise fitting the birth, death and growth data (solid), and the upper (dashed) and lower bounds (resulting in extinction, $S \equiv 0$), based on 1 S.E. The solutions vary quite considerably and illustrate the potential for extinction or attaining triple the expected population.

most important mechanisms. Instead, we consider the maximum and minimum monthly mean temperatures recorded in the UK between 1961 and 1990 (National Climate Data Centre, 2000) which were averaged over this period in order to capture the underlying dynamics. Thus, the temperature dependent parameters $g(T)$, $d(T)$ and $\rho(T)$ have also been fitted to these extremes, to illustrate the effect of a prolonged period (several years) of excessively hot or cold weather. The simulation results are plotted in Fig. 5. Note that here we do not plot the upper and lower error bounds as in Fig. 4.

Of most significance are the large variations in distribution, which reflect the strong temperature dependence. It would be very revealing to compare such qualitative differences with appropriately refined field data (beyond the scope of this paper). In practice, a large range of dynamics may be generated by imposing variations in the climate, dynamics which are inherently linked to the large time delay. Note that extreme temperatures are not favoured by slugs (see South, 1982), and we might expect populations to flourish when the winter/summer temperatures are higher/lower than we might expect. If the converse is true, then we would expect the double impact of reduced egg production in the summer (due to excessive heat) combined with an increased decay rate in winter (due to the cold) to have a detrimental impact on the slug population. Furthermore, the effect of alternating good and bad years (for which the delay plays a most important role) also drives the solution to oscillate wildly (results not shown here).

4.6. Perceived slug damage

To understand why slugs appear to cause more damage at certain times of the year we need to consider not only the quantity of slugs but also their food consumption, which will not be constant throughout the

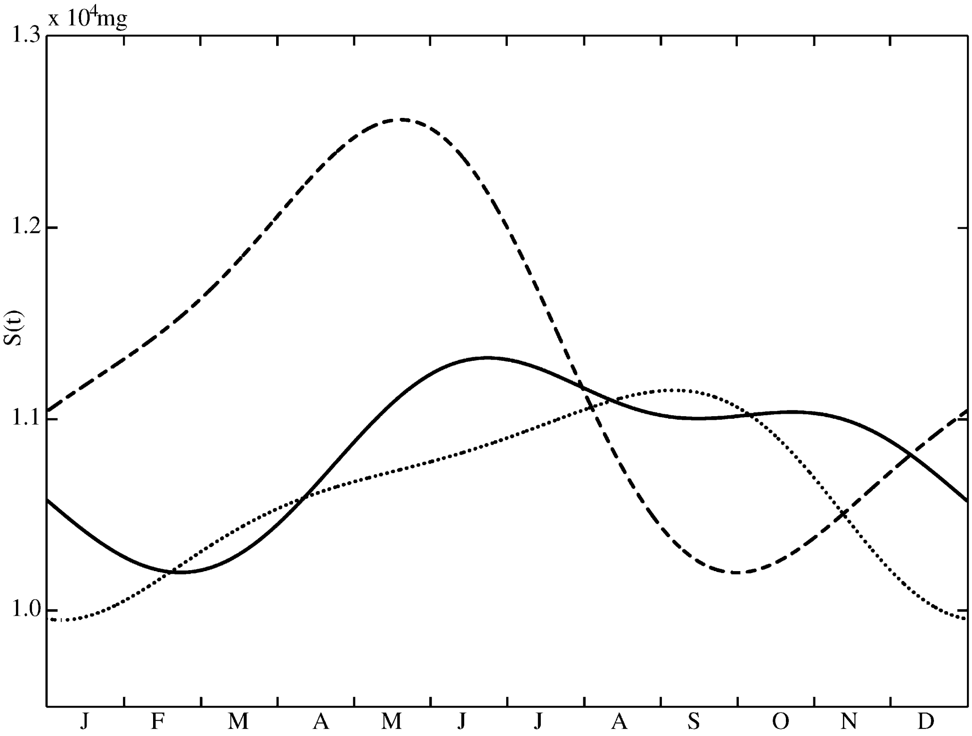

Fig. 5. The slug population at mean monthly temperatures averaged over 1961–1990 (solid), compared to results when temperatures are instead taken at the maximum (dashed) or minimum (dotted) mean monthly temperature attained during that period.

year as it depends on the growth rate $g(t)$ of each individual.

As one *measure* of the vegetation consumed, $V(t)$, one might take the total growth of slug biomass at any given time. Hence, we set

$$V(t) = g(t)S(t)\,\mathrm{mg\,week}^{-1}\,\mathrm{m}^{-2}, \tag{18}$$

and plot $V(t)$ for a simulation with the standard parameter values in Fig. 6. This measure is clearly a lower bound on the true damage since it assumes that the metabolic efficiency of slugs of varying size is constant and, more importantly, that crop damage does not affect the future growth of the crop. To correctly measure crop damage one must also construct a model of crop growth. However, this lower bound on crop damage does provide some valuable insight: even if the actual slug biomass varies relatively little, the observed slug damage can fluctuate dramatically, giving peaks in the spring and autumn.

However, in terms of commercial damage, it may be more pertinent to model slug numbers, since most vegetables and fruit may be made unsalable by a single defect (damage caused by a single slug).

4.7. Predation

The analytical results in Section 3.4 showed that the slug population could be bounded by predation alone in the absence of resource limitations, provided the predation was sufficiently strong (sufficiently large $\hat{a}$ and small $\hat{b}$). Simulations using a time independent predation term, of the form (2), produce results that are similar to those with a (time independent) carrying capacity, and result in qualitatively similar slug dynamics throughout the year.

More interesting behaviour results if we consider the biology of carabid beetles in the field. *P. melanarius* emerges from June onwards, which results in relatively little predation in the spring. This variation in the level of predation (especially in the absence of other limiting factors) introduces new dynamics into the population and has a significant effect on the

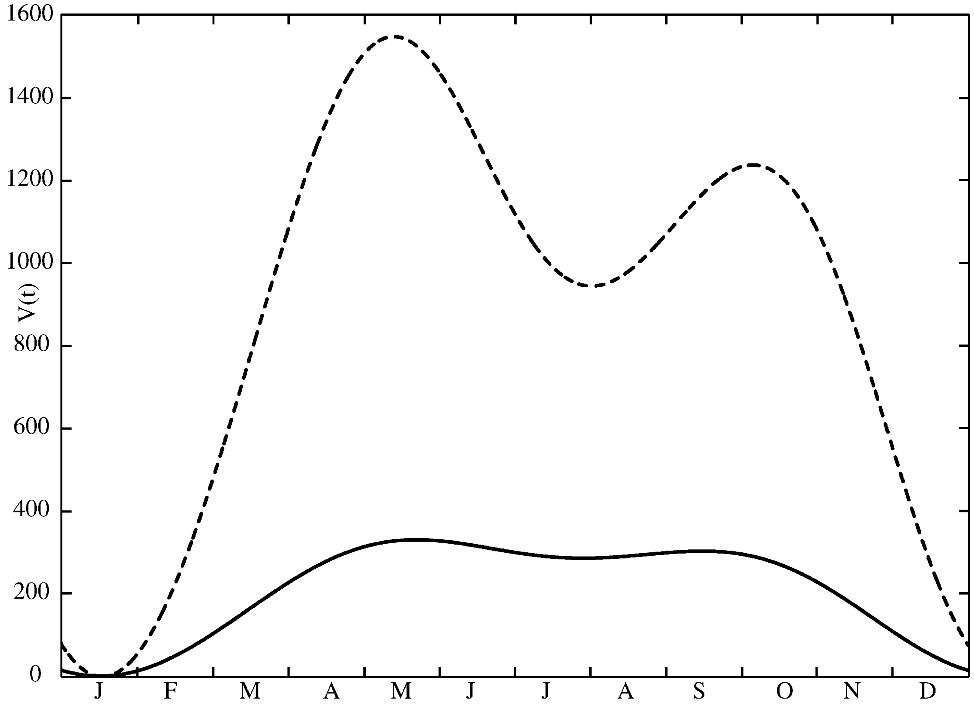

Fig. 6. The rate of consumption of vegetation per unit area, $V(t)$ (solid), and the upper bound (dashed) defined by 1 S.E. of the data. The vegetation consumed is assumed to be proportional to the total growth of the current biomass, resulting in much larger fluctuations in observed damage than in the actual population biomass.

population distribution, even when its effect on the mean population is small. However, qualitative solutions must suffice at this stage owing to the lack of quantitative field data.

The effect of beetle predation is governed by their choice of prey size (see Section 2.4). In particular, the destabilising effect of juvenile predation in adult models was previously highlighted. Simulations of these models produce periodic and more complex behaviours as discussed in Section 3.4.

Adult slugs may be predated by birds and other animals, as well as by various species of beetle. Furthermore, the analytical results from Section 3.5 indicated that, for certain regions in the $(\bar{a}, \bar{b})$ parameter space, predation in the presence of resource limitation could result in the bistability of positive steady states. Moreover, simulations in the presence of non-autonomous parameters reveal a switching behaviour between low (contained) and high (outbreak) periodic solutions. Fig. 7 plots the two possible locally stable asymptotic solutions of the model for limited resources with adult predation by beetles, using the non-autonomous parameters given by Eq. (13). However, a small reduction (<8%) in the predation saturation rate results in the loss of bistability for a short period of the year, and this is sufficient for the low level ("contained population") solution to become unstable. The population grows rapidly to the higher ("outbreak") solution – a switch which is difficult to reverse. Once solutions have grown, they remain in a relatively large stability basin; this can best be seen by considering the intersection of the curves

$$(\tilde{r} - \mu) - \frac{S}{K} \quad \text{and} \quad \frac{\hat{a}S}{\hat{b}^2 + S^2}.$$

Intersection points represent equilibria and, in the undelayed model at least, the boundaries of the stability basins around a stable equilibrium are indicated by the values of adjacent unstable equilibria. The extensions of stability basin results to models with delays are discussed in the Appendix A.

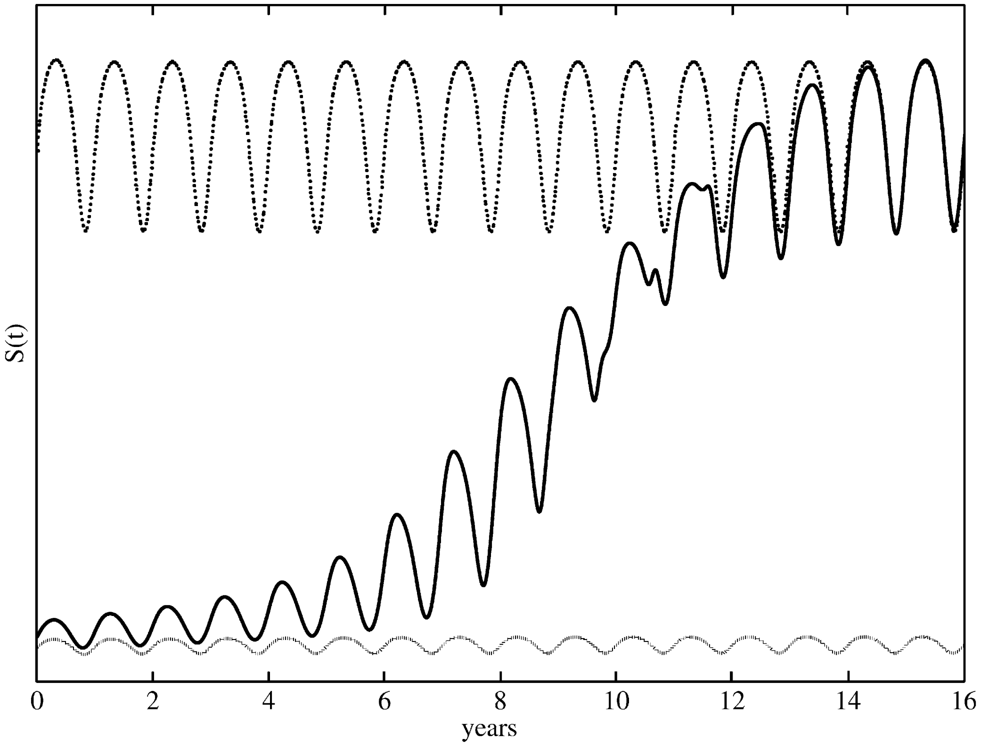

Fig. 7. Bistable and transient solutions. Small changes in the predation rate may significantly affect the resultant slug population. When predation is sufficiently strong, there exist two stable asymptotic solutions, so that the population converges to a solution that is dependent on the initial conditions. With a slight reduction in predation (a), however, the lower "contained" solution (shaded line) becomes unstable, so that all initial conditions converge to the higher "outbreak" solution (dotted line). Thus a small (less than 8%) reduction in the predation capacity results in a dramatic increase in the slug population (solid). As both solutions are stable, the population will remain high in the outbreak state, even if predation increased to its original value. To return the population to its original low contained state, the solution would have to be forced low, not just at one point in time but for a sustained period due to the delay.

In Fig. 7 this outbreak is driven by a small reduction in the predation response, $\hat{a}$, over a number of years, although it could equally well result from an increase in the reproduction rate ($\tilde{\rho}$) or carrying capacity measure (K), or a decrease in the decay or predator response rates (μ or $\hat{b}$). If the population biomass is large, then small variations in these parameters will alter the solution only slightly. If we have low slug numbers, however, as is usually desired, a relatively short period of time in which conditions are unusually favourable for slugs (or unfavourable for predators) may be sufficient to cause an outbreak. Even if the predation were to increase again, the population would remain at the relatively high level due to the delay. This observation could have important implications for the design of efficacious biocontrol measures.

5. Discussion

In this paper, we have developed and analysed a set of models for the dynamics of the slug *D. reticulatum*, which is applicable to both the total slug biomass and the population number.

Analytical techniques were used for a model of a controlled environment, which can give an indication of the asymptotic solution behaviour at any given time in a variable environment. The numerical experiments (using laboratory and field data) and analytical results were employed to elucidate the possible dynamics of slug populations under various conditions and to explore the significance of various aspects of the life cycle of slugs.

We have found that a wide range of solution behaviour is possible if the experimental data, that are required to construct the parameter values, are allowed to vary by 1 S.E. The associated parameter range allows for behaviour from extinction to almost triple the population for the standard parameters. In particular, we find that large amplitude oscillations are present as a result of the interaction of variable and delayed reproduction, death and growth. A larger biological data set on slug life cycle characteristics would be beneficial for comparative studies of theory with experiments.

Results based on the expected and extreme monthly temperatures indicate that variations between years produce different population distributions over the course of a year, although not with significantly different amplitudes. Numerical simulations suggest that unpredictable (large amplitude) solutions can result if we consider different conditions in consecutive years. The hypothesis that small changes in conditions can result in large variations from year to year is also supported by a discrete model based on egg production (Schley and Bees, 2002).

Results suggest that some of the perceived variation in slug numbers in the field at different times of the year may *in part* be due to the large differences in slug growth rate. Thus, even when the slug biomass remains relatively constant, the amount of damage to vegetation varies greatly. Since most slugs remain underground for much of the time and only emerge to eat, standard trapping methods may only reflect the number of actively feeding slugs, rather than the total number of slugs. Greater emphasis must be given to more sophisticated techniques such as soil sampling and flooding (e.g. Glen et al., 1993), since crop damage may not be an accurate measure of the population.

As predicted by the analytical results, populations may be bounded by resource limitation or predation, provided it is sufficiently strong. Otherwise, some other limiting factor (beyond the natural birth/death cycle) may be required, such as parasitism or disease promoted by overcrowding. Variable predation results in far more dramatic dynamics than those associated with a constant limitation, and the same is true when the carrying capacity is time dependent. Populations limited by predation can be qualitatively similar to those limited by resources or disease, and so it is not possible to infer from the model which factors limit slug populations in the natural environment. However, the results do suggest that the population is ultimately limited by some external factor beyond intrinsic reproduction, growth and decay.

The presence of even relatively low predation has been shown to induce bistability: the coexistence of stable low (contained) and high (outbreak) solutions. Small changes in the parameters can result in a switch between solutions, usually associated with a rapid change in the average yearly population. To return the population to its contained state, it must be suppressed for a sustained period of time (due to the time delay present in the reproductive cycle). This is an important factor when control strategies are to be considered. It may, for example, be detrimental to use treatments which have a longer recovery time for natural controls than for target species. Predators must also recover sufficiently quickly to maintain the population at the contained level.

We have shown that juvenile predation is capable of inducing oscillatory and possibly chaotic solutions in the adult model, resulting in large amplitude solutions. This can add a further time scale to the system that is incommensurate with other delay and annual forcing time scales and thus adds complexity to the resulting dynamics. There is good evidence that juvenile predation by carabid beetles is predominant in the field, which increases the importance of this particular model and the validity of the results.

It is now clear that close attention should be paid to all the ecological factors when attempting to explain the observed dynamics of slug populations. The specific environment, and particularly the variation in its favourability for slugs, appear crucial in determining both the population magnitude and its fluctuations throughout the year. The natural dynamics of slugs in their undisturbed state appear relatively simple, and indicate unbounded growth in the presence of unlimited resources. However, limiting factors are clearly an important part of the dynamics of slugs in the field, although we have shown that restrictions of very different origins may produce qualitatively similar results.

It is a hard task to obtain good and reliable data on the life cycle of slugs, and often the most available data will govern the choice of model type. In general, the choice of juvenile, adult or combined model should be determined by the population that has the greatest numbers (or is easiest to measure). A clear prerequisite for the development of accurate predictions of populations, for which predation is considered a significant factor, is the estimation of the predation parameters.

In all models the effect of the temporal delay has been shown to be of importance. In addition to influencing the asymptotic solution of a system, it has particular significance with regard to the transient behaviour. When determining the evolution of the system, such as whether we attain an "outbreak" or a "contained" population, knowledge of the previous years population distribution is a prerequisite. This may result in transient oscillations of much greater amplitude than otherwise expected. In particular, the delay can induce stable periodic solutions. Such effects interact with other mechanisms in the non-autonomous system. In such a model, the delay introduces a memory into the system, and so relays the impact of previous environmental conditions onto the present population.

The large fluctuations observed in slug populations may also have a spatial element (see for example the interaction with beetles, Bohan et al., 2000). Modelling this aspect of *D. reticulatum* populations is a work in progress. Such spatial systems may be necessary in order to take into account the dynamics of "patchy" (Barnes and Weil, 1944) populations. Although there is evidence for limited aggregation in certain environments, such as grassland (South, 1965; Mordan, 1973), other environments such as woodland appear to have random/over-dispersed distributions (Jennings and Barkham, 1975). Moreover, the evidence in arable crops is inconclusive (South, 1965). The vertical distribution of slugs in the soil (e.g. South, 1964; Warley, 1970) is unlikely to require explicit attention, since feeding and other interactions, such as predation or mating, generally occur on the surface.

Managing populations of slugs in agriculture is most important. However, the best strategy for doing so is, at best, unclear. A question of fundamental importance is when and how to apply controls. In particular, should one treat the slugs when their numbers are high or attempt to eradicate the pest when they are environmentally stressed. The construction of efficient and efficacious control strategies for the management of slugs is the subject of further work (Schley and Bees, 2001).

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Appendix A

In this section, we consider the constraints on the initial conditions of the delay differential equation which are necessary in order to predict the subsequent solution behaviour. In the case when there is no delay, we need only consider the single initial value at $t = 0$. With delay, however, all past values which are referred to are required. Here, we present a series of useful theorems, the proofs of which are available from the authors on request.

Consider the model equation

$$\frac{\mathrm{d}s(t)}{\mathrm{d}t} = s(t-\tau) - F(s(t)), \tag{A.1}$$

where

$$F(s(t)) = \mu s(t) + \frac{as^2(t)}{b^2 + s^2(t)}, \tag{A.2}$$

with initial conditions

$$s(t) = \psi(t),\, t \in [-\tau, 0]. \tag{A.3}$$

The case when there exists a positive equilibrium is of interest, and thus consider

$$\mu \in \left(\frac{1-a}{2b}, 1\right) \tag{A.4}$$

(see Table 2 for equilibria and stability when this condition is not satisfied).

In the absence of delay (τ), the solution is governed by the the initial value $s(0)$. Solutions from Section 3.4 may be summarised as follows:

Theorem 1. *When* $\tau = 0$, *solutions of* Eqs. (A.1)–(A.4), *with initial conditions* $\psi(t) \equiv \psi,\ t \in [-\tau, 0]$:

converge to s_1^* *if* $0 < \psi < s_2^*$; *or become unbounded if* $\psi > s_2^*$, *where*

$$s_{1,2}^* = \frac{a \mp \sqrt{a^2 - 4b^2(1-\mu)^2}}{2(1-\mu)}.$$

Thus, there is a clear threshold, namely $s_2^*(a, b, \mu) > 0$, which separates solutions by their initial conditions. The presence of a delay may destabilise the equilibrium and produce periodic (or even chaotic) solutions, but solutions may still be separated—by their initial conditions—into those which remain bounded and those which do not.

The following theorem confirms what one might expect intuitively:

Theorem 2. *Solutions of Eqs. (A.1)–(A.4): remain bounded above by* s_2^* *if* $\psi(t) < s_2^*\, \forall t \in [-\tau, 0]$; *and become unbounded if* $\psi(t) > s_2^*\, \forall t \in [-\tau, 0]$.

The case of interest is, therefore, when initial conditions are both above and below the threshold value. In practice, we may usually assume that the solution will behave as described above if the initial conditions $\psi(t)$ remain above (or below) the threshold for a "sufficiently" large proportion of the time $t \in [-\tau, 0]$. This statement is sufficiently vague so as to allow for the strong dependence on the actual distribution $\psi(t)$ and, in particular, the size of its variation.

Sharp criteria on the initial conditions have not been found except for very simple delay equations. Stricter criteria than those above may be derived by assuming that any non-constant solutions (of the autonomous equation) will be quasi-periodic with a period $T < \tau$. This is a reasonable assumption in most cases since the system is forced by a delayed term with time lag τ. Therefore, we look for criteria such that $s(\tau) < s(0)$, so that boundedness may be derived by induction on τn $(n \in \mathbf{Z}^+)$.

For small amplitude variations in the initial conditions we may, under certain conditions, derive results based on the mean. If $\psi(t)$ is approximately constant, the case to be considered is when $\psi \approx s_2^*$, since otherwise it may be assumed that either $\psi(t) > s_2^*$ or $\psi(t) < s_2^*$ for all $t \in [-\tau, 0]$, and we may apply Theorem 2.

Theorem 3. *If* $\mathrm{d}F(s)/\mathrm{d}s|_{s=s_2^*} \ll 1$, *solutions of Eqs. (A.1)–(A.4), with initial conditions* $\psi(t) \approx s_2^*$, $t \in [-\tau, 0]$ *satisfy*:

$$s(\tau) < s(0) \quad \text{if } \bar{\psi} < s_2^*;$$
$$s(\tau) > s(0) \quad \text{if } \bar{\psi} > s_2^*;$$

where $\bar{\psi}$ *is the mean value of* $\psi(t)$ *on the interval* $[-\tau, 0]$:

$$\bar{\psi} = \frac{1}{\tau}\int_{-\tau}^{0} \psi(t)\,\mathrm{d}t.$$

Our final results do not place any preliminary restraints on our parameters, but will, therefore, be more restrictive on the initial conditions.

Theorem 4. *Solutions of Eqs. (A.1)–(A.4) satisfy* $s(\tau) > s(0)$ *whenever*

$$\bar{\psi} < F(\psi_{\max}\tau + \psi(0)),$$

where

$$\psi_{\max} = \max_{t\in[-\tau,0]}\psi(t).$$

The following provides an upper bound for all initial conditions which will give bounded solutions.

Theorem 5. *Solutions of Eqs. (A.1)–(A.4) will remain bounded above by* s_2^* *for all* $t > 0$ *whenever*

$$s_2^* - \mathrm{e}^{-\mu t}\psi(0) > \int_0^t \psi(r-\tau)\,\mathrm{e}^{\mu(r-t)}\,\mathrm{d}r. \tag{A.5}$$

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