



A Formal Derivation of the “Beddington” Functional Response

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In ecological modeling the interaction between a predator and its prey, is usually implemented as a linear or saturated function of the prey density. The main advantages of such a “functional response” are its simplicity, general applicability, and well understood mechanistic basis. In systems where predators compete directly for the available prey however, the functional response should depend not only on the prey density but also on the predator density. We aim here to devise a simple and generic “predator-dependent” functional response. We derive such a functional response by making quasi-steady-state assumptions for models, in which we allow predators and prey to form interaction complexes. We end up with the—previously proposed—“Beddington” functional response. Because of our formal derivation this simple predator-dependent functional response is now based on clear mechanistic reasoning. The direct predator interference of this functional response emerges from the interaction between a predator and a prey, and not from direct predator-predator interactions. We conclude however that, although the Beddington functional response is generic for a two-dimensional system of one prey interacting with one predator, it is difficult to generalize it to higher dimensional systems consisting of several prey and predator species.

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1. Introduction

Most predator prey interactions are modeled with a linear functional response or with the saturated Holling type II functional response. Following the introduction of the ratio-dependent functional response by Arditi & Ginzburg (1989) there has been an extended debate between its proponents (Arditi & Ginzburg, 1989; Arditi & Akçakaya, 1990; Ginzburg & Akçakaya, 1994; Berryman, 1992) and its opponents (Oksanen *et al.*, 1992; Diehl *et al.*, 1993; Gleeson, 1994; Abrams, 1994). Because the ratio-dependent function lacks a mechanistic basis, and because it allows for artificial model behavior when predator and prey densities are low, we are also opposed to the ratio dependent view.

The most important advantage of the Holling type II functional response is that it is mathematically and mechanistically simple. The Holling type II function

can be derived mechanistically and requires only the intuitive assumption that a predator cannot eat an unlimited amount of prey per unit of time. This simplicity allows the Holling type II functional response to be employed in a wide variety of models, ranging from simple two-dimensional models with one predator and one prey species to higher dimensional models involving, say, n prey and m predator species.

The classic “Paradox of enrichment” paper (Rosenzweig, 1971) is based upon a Lotka–Volterra model without predator interference, and upon a Holling type II functional response. Such a model has a vertical predator nullcline and a humped prey nullcline. The result of Rosenzweig’s model was that enriching an aquatic ecosystem by increasing the carrying capacity of the prey may destabilize the non-trivial equilibrium point and give rise to high amplitude oscillations. In a stochastic environment such limit cycles can lead to the extinction of one of the species, hence the *paradox* of enrichment

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(Rosenzweig, 1971). The same simple model also predicts that the eutrophication is reflected only by an increase in the predator density. The biomass of the prey is not expected to increase. The latter result however, is an artifact of the vertical predator nullcline of this over-simplified model. Rosenzweig was right to illustrate his Paradox of Enrichment with the simplest model available, i.e., one without predator interference.

Field observations in aquatic ecosystems cast doubt on the occurrence of the Paradox of Enrichment for algae-zooplankton interactions in eutrophic systems. Limit cycles in natural systems are typically of limited amplitude (i.e., $2 \leq N_{\max}/N_{\min} \leq 4$), and the amplitude does not seem to correlate with nutrient richness (McCauley & Murdoch, 1987, 1990). If realistically estimated parameters are applied Rosenzweig's simple model predicts large amplitude oscillations. In order to obtain a model behavior that is more in line with these field observations, several modifications and extensions of the Lotka-Volterra Holling type II models have been proposed. Some examples are prey inedibility (McCauley *et al.*, 1988; Leibold, 1989), size- or age-structured interactions (Mittelbach *et al.*, 1988; Persson *et al.*, 1992; De Roos *et al.*, 1990), spatial heterogeneity (Scheffer & De Boer, 1995), and predator interference (Persson *et al.*, 1992; Arditi & Ginzburg, 1989).

The simplest way of obtaining predator interference is to introduce a self-limitation term for the predators (Berryman, 1992). Such a form of predator interference is however independent of the prey density. It seems more realistic to have strong interference when the amount of available prey per predator is low. This ratio of prey per predator, is the one on which the ratio-dependent functional response is based (Arditi & Ginzburg, 1989; Arditi & Akçakaya, 1990; Ginzburg & Akçakaya, 1994; Berryman, 1992). Indeed, in Appendix A.1 we demonstrate that ratio dependent models cannot be destabilized by eutrophication, i.e., by increasing the carrying capacity only. Additionally, because ratio-dependent models have a diagonal predator nullcline, both prey and predator increase with eutrophication.

Another, and in our opinion better, functional response that allows for predator interference is the one proposed by Beddington (1975). The Beddington functional response lacks the artificial behavior of ratio-dependent models, and can be derived mechanistically (Ruxton *et al.*, 1992). The predator nullcline of a Beddington model is also slanted, and hence allows for the same results as the ratio-dependent model, with the exception that eutrophication can destabilize the non-trivial equilibrium.

Recently we demonstrated that the Beddington functional response can also be derived from predator-prey interaction lacking explicit interference (Borghans *et al.*, 1996). This derivation followed from an extension of the conventional Michaelis-Menten quasi-steady-state (QSS) approximation for a replicating substrate. In this way we developed models where the replication of the predator is "catalysed" by the prey. Here we repeat our previous analysis more rigorously in an ecological context by allowing for predator handling time, growth of the prey and death of the predator.

2. Properties of the Beddington Functional Response

The general model for a predator prey interaction is

$$\frac{dN}{dt} = f(N)N - g(N, P)P, \quad (1a)$$

$$\frac{dP}{dt} = cg(N, P)P - mP, \quad (1b)$$

where the variables N and P denote the prey and predator density, respectively. The parameter c is a conversion efficiency and m is the mortality rate of the predators.

The function $f(N)$ describes the growth of the predator population, which is most often modeled as a logistic growth term $f(N) = r(1 - N/K)$, where r denotes the growth rate of the prey and K is the carrying capacity. The function $g(N, P)$ describes the functional response. The Beddington functional response is

$$g(N, P) = \frac{bN}{h + N + wP}, \quad (2)$$

where the parameter b is the maximum number of prey that can be eaten by a predator per unit of time, h is a saturation constant, and w scales the impact of the predator interference. For $w = 0$ the Beddington function simplifies to the Holling type II function.

In Fig. 1 we analyse this model graphically by phase plane analysis. Following Arditi & Ginzburg (1989) we distinguish two qualitatively different parameter regions, i.e., the "limited predation" case [Fig. 1(a)], and the "humped isocline" case [Fig. 1(b)]. The two cases can be distinguished by the slopes of the production curve $f(N)$ and the maximum consumption curves, i.e., $Pg(N, P)$ for $P \rightarrow \infty$. In Fig. 2 we plot these functions as a function of N . Near the origin, i.e., for $N \rightarrow 0$, their slopes are r and b/w respectively. When $r < b/w$ the production and consumption curves may intersect at two points and

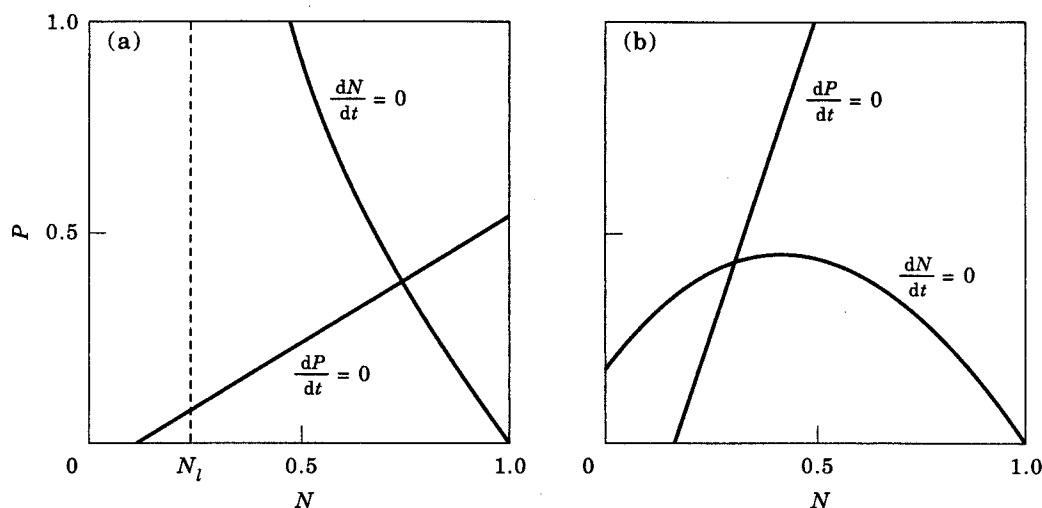


FIG. 1. Nullclines of the Beddington-model for two qualitatively different parameter regions. In the "limited predation" configuration (a) the prey isocline has a vertical asymptote at $N = N_l$. Panel (b) shows the humped isocline case. Parameters panel (a): $r = K = 1$, $b = 0.85$, $h = 0.1$, $w = 1$, $c = 0.1$, and $m = 0.05$. In panel (b) $b = 1$ and $w = 0.4$ are changed, all other parameters are identical. See the text for further explanation.

the humped isocline case is obtained; otherwise there will be just one point of intersection and one will obtain the limited predation case (Fig. 2). For less than maximum predation the initial slope of the consumption curve is $b/(h/P + w)$, which increases with P [see Fig. 2(b)]. Therefore, for low predator densities there is only one intersection point, implying that the prey nullcline cannot pass through the origin.

Additionally, like the Holling type II model, but unlike the ratio-dependent model, the Beddington model has a minimum prey density, below which the predators cannot survive (see Fig. 1).

Because the Beddington model has a slanted predator isocline, it tends to be more stable than the Holling type II model. For the limited predation case, i.e., $r > b/w$, the equilibrium cannot be destabilized

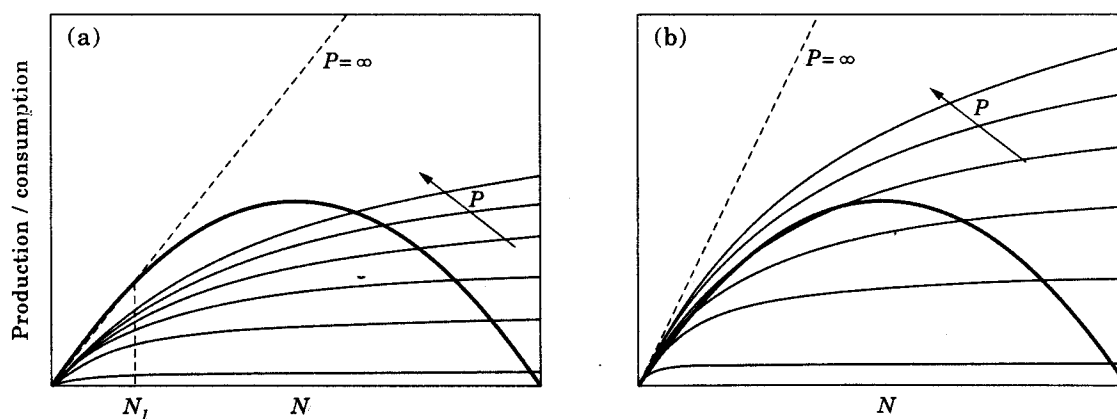


FIG. 2. Production and Consumption curves of the Beddington model. The heavy lines depict the production curve $f(N)$, the light lines the consumption curves $Pg(N, P)$, and the dashed lines the maximum consumption curves, i.e., $Pg(N, P)$ for $P \rightarrow \infty$. In panel (a) we set $r > b/w$ such that the slope of the production curve exceeds that of the maximum consumption curve. For each value of P there can therefore be only one point of intersection, and all intersection points occur for $N > N_l$. This yields the limited predator nullclines of Fig. 1(a). In panel (b) we set $r < b/w$. Now we have either one or two points of intersection for every value of P , and we obtain the humped isocline case of Fig. 1(b). Similar results were found for the ratio dependent functional response (Arditi & Ginzburg, 1989).

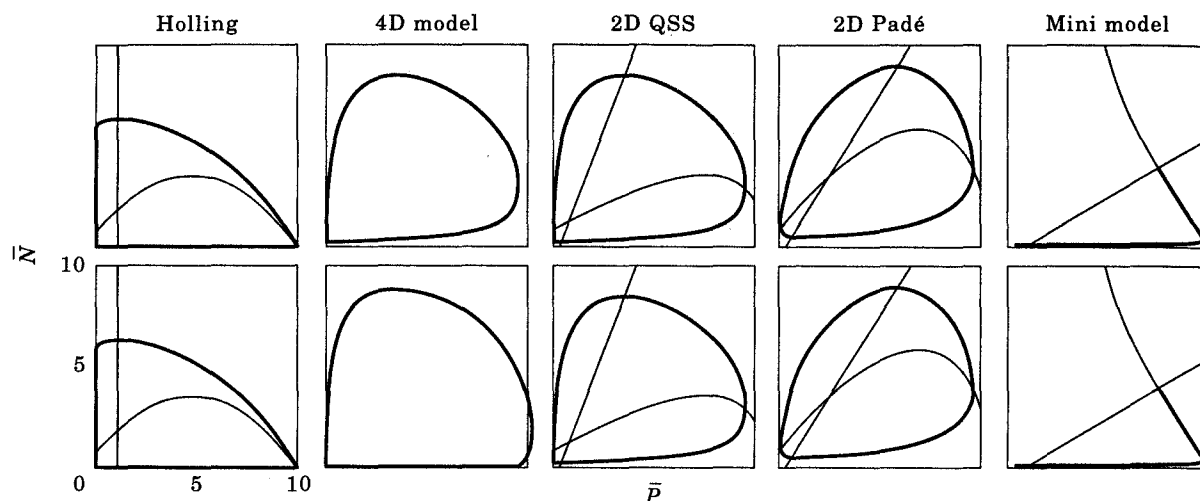
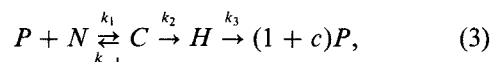


FIG. 3. Phaseplot (thick black lines) and nullclines (thin black lines) for five model types (columns) and two escape probabilities (rows) for a parameter setting for algae zooplankton interactions (Scheffer & De Boer, 1995). In the first row the probability of escaping is 90% ($k_{-1} = 36.0$, $k_2 = 0.4$), in the second row 10% ($k_{-1} = 0.004$, $k_2 = 0.4$).

by increasing the carrying capacity K only. The humped isocline case destabilizes at higher values of K than does the Holling type II model. Conversely, the ratio dependent model cannot be destabilized at all by increasing K only (see Appendix A.1).

3. Derivation of the Beddington Functional Response

Our approach is to derive a functional response from reaction schemes like:



where P denotes predator density, N prey density, C an interaction complex of predator and prey, and H the density of handling predators.

A predator handling a prey is a well-established concept in ecology. The interaction complex of predator and prey requires further explanation. We think of the complex as a prey being in the "field of attention" of a predator. The general argument is that a predator "locks in" on a certain prey. This prey is still alive, and can still escape, but no other predator will lock in on it: As an example one can think of a "sit and wait" predator, that locks in on a nearby prey. The predator is focused on that single prey and no other predator will attempt to catch that prey. Such a predator and prey can be regarded as an interacting complex that is not interacting with other predators and prey. Another example is a predator chasing a prey. Again there is a short period in which the prey is still alive, and has the possibility to escape. In this short period neither the prey nor the predator is involved in interactions with other predators and prey. The complex need not be a direct interaction,

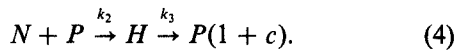
but can also arise from a spatial distribution. For example a territorial predator can be regarded as being in complex with the prey in its territory. The predator will only catch prey in its own territory, and prey in this territory are protected from other predators. Such a complex falls apart when the prey leaves the territory.

Thus, in eqn (3) the parameter k_1 denotes the frequency with which predators and prey meet, k_{-1} is the rate of prey escape, k_2 is the rate of prey capture, $1/k_3$ is the handling time, and c is a conversion factor. This scheme is inspired by the well-known reaction scheme for enzyme kinetics, where an enzyme and a substrate molecule form a complex which can either fall apart, or produce the intended product in an irreversible reaction. We here replace substrate by predator, enzyme by prey, and interpret the product formation as an increase in predator density. The handling predator is added to the scheme, because it is a well-known concept in ecological models, and because it allows us to derive a more general functional response. To show how a functional response can be derived from such a reaction scheme, we will start with a simplified example.

3.1. HOLLING TYPE II

The mechanistic argument for the Holling type II functional response is the handling time. The Holling function can formally be derived by splitting the available time into time spent searching for the prey and time spent handling the prey, and by calculating the net effort in the total time (Metz & Diekman, 1986; Stephens & Krebs, 1986). To set the stage for the work presented below we here derive the Holling

function from a simplified version of scheme (3), i.e., from



As a general example we assume logistic growth for the prey and a linear turnover for the predators. This yields the ODE model

$$\frac{dN}{dt} = rN(1 - N/K) - k_2NP, \quad (5a)$$

$$\frac{dP}{dt} = -mP + k_3(1 + c)H - k_2NP, \quad (5b)$$

where r denotes the intrinsic growth rate of the prey, K the carrying capacity and m is the death rate of the predator (which we assume to be equal for both handling and searching predators).

Defining total number of predators as

$$\bar{P} \equiv P + H, \quad (6)$$

and simplifying the system by making a quasi-steady-state assumption for eqn (5c) we obtain

$$H = \frac{N\bar{P}}{k_h + N}, \quad \text{where } k_h = \frac{k_3 + m}{k_2}. \quad (7a, b)$$

Thus, the model can be reduced to the well-known

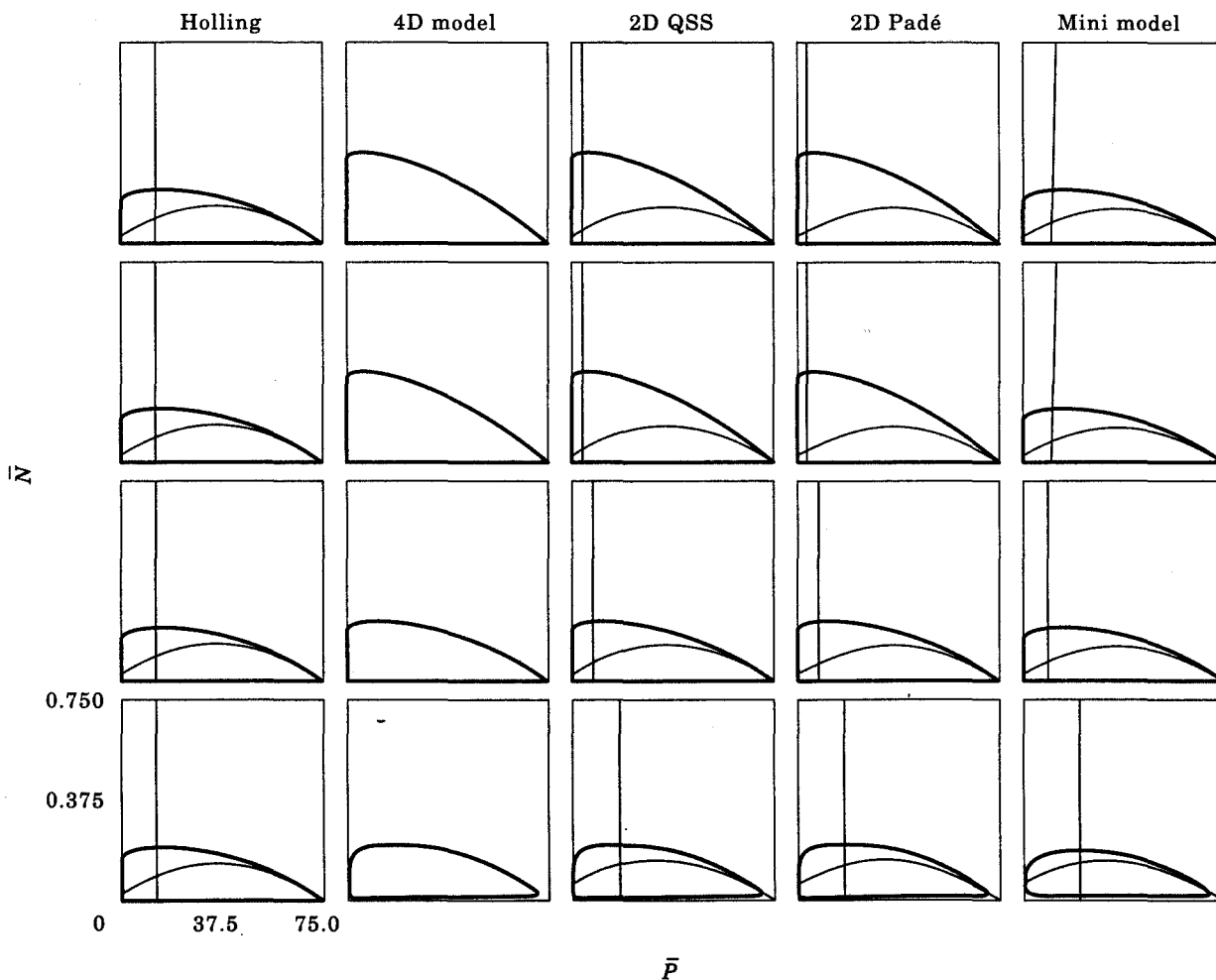


FIG. 4. Phaseplot (thick black lines) and nullclines (thin black lines) for five model types (columns) in a parameter setting for Microtine rodent Mustelid interactions (Hanski & Korpimäki, 1995). Predator interference is high in the two upper rows and low in the two lower rows ($\epsilon \approx 0.93$ in row 1 and 2, $\epsilon \approx 0.18$ in rows 3 and 4). Escape probabilities are high (90%) in rows 1 and 3, and low (10%) in rows 2 and 4.

two-dimensional system

$$\frac{dN}{dt} = rN(1 - N/K) - (k_3 + m) \frac{N\bar{P}}{k_h + N}, \quad (8a)$$

$$\frac{d\bar{P}}{dt} = -m\bar{P} + ck_3 \frac{N\bar{P}}{k_h + N}, \quad (8b)$$

in which we easily recognize the disk equation as proposed by Holling (1959).

3.2. PREDATOR-DEPENDENT MODEL

We now perform the same analysis for the full version of scheme (3). Additionally, we extend the above analysis by changing variables into total numbers of predators and total numbers of prey (Borghans *et al.*, 1996). This yields a predator-dependent functional response. Note however that we do not introduce explicit predator interference into scheme (3), i.e. the interference emerges naturally from scheme (3).

The ODE model that follows from scheme (3) is

$$\frac{dN}{dt} = rN(1 - N/K) - k_1PN + k_{-1}C, \quad (9a)$$

$$\frac{dP}{dt} = -mP + k_{-1}C + k_3(1 + c)H - k_1PN, \quad (9b)$$

$$\frac{dH}{dt} = k_2C - k_3H - mH, \quad (9c)$$

$$\frac{dC}{dt} = k_1NP - k_{-1}C - k_2C, \quad (9d)$$

where we make the same assumptions as in Section 3.1. An additional assumption is that the complexes are short lived, which allows us to neglect the death rate of the predators and preys in the complex (which greatly simplifies the analysis).

Reducing eqn (9) to a two-dimensional model with a simple functional response requires three simplification steps. First we make a quasi-steady-state (QSS) approximation to decrease the number of variables from four to two. Thereafter, we simplify a complicated quadratic expression for C with a Padé approximation [see our previous paper (Borghans *et al.*, 1996) and Baker & Gravis-Morris (1984) for an explanation of the Padé approximation]. Finally, we neglect some terms in the model to arrive at the Beddington model. In total we thus have four models that we will refer to as the "full" model, the "QSS" model, the "Padé" model and the "minimal" model. The full model is given by eqn (9).

Changing variables to total number of prey and total number of predators, i.e.,

$$\bar{N} \equiv N + C, \quad \text{and} \quad \bar{P} \equiv P + H + C, \quad (10a, b)$$

and making a QSS assumption for eqns (9c) and (9d), i.e.,

$$k_2C - k_3H - mH = 0, \quad (10c)$$

$$k_1((\bar{N} - C)(\bar{P} - H - C) - k_mC) = 0, \quad (10d)$$

we obtain

$$H = \frac{C}{k_h}, \quad \text{and} \quad C = \frac{1}{2}(\bar{P}\epsilon + \bar{N} + k_m\epsilon \pm \sqrt{(\bar{P}\epsilon + \bar{N} + k_m\epsilon)^2 - 4\bar{P}\bar{N}\epsilon}), \quad (10e, f)$$

where k_h is defined by eqn (7b), and

$$k_m = \frac{k_{-1} + k_2}{k_1}, \quad \epsilon = \frac{k_h}{k_h + 1} < 1. \quad (10g, h)$$

Since the positive root violates the condition $C \leq \bar{N}$ given by the conservation law (see the Appendix A.2), we only consider the negative root of eqn (10f). Thus, we obtain our two-dimensional QSS system, i.e.,

$$\frac{d\bar{N}}{dt} = r(\bar{N} - C)(1 - (\bar{N} - C)/K) - k_2C, \quad (11a)$$

$$\frac{d\bar{P}}{dt} = -m(\bar{P} - C) + ck_2 \frac{k_3}{k_3 + m} C, \quad (11b)$$

where C is defined by the negative root of eqn (10f). This model is too complicated for two reasons. First, the square root term of eqn (10f) is too complex for the model to be elegant. Second, the logistic growth and the predator turnover terms still depend on the complexes. The next two simplifications serve to eliminate both complications.

The complicated solution for C , i.e., eqn (10f), can be simplified by a Padé approximation (Borghans *et al.*, 1996). This yields

$$C \approx \frac{\bar{N}\bar{P}\epsilon}{\bar{N} + \bar{P}\epsilon + k_m\epsilon}, \quad (12a)$$

which holds when $\bar{N}$ is either large or small compared with $\bar{P}$ (Borghans *et al.*, 1996). Even when $\bar{N} = \bar{P}$ the approximation should be reasonable whenever $1 \ll 2 + k_m/\bar{P}$ (Borghans *et al.*, 1996). Thus we expect our Padé model, i.e., eqns (11) and (12a), to be a reasonable approximation of the QSS model. Note that for $ek_m = h$ and $\epsilon = w$, eqn (12a) is equivalent to the Beddington functional response given in eqn (2). With respect to the predation terms, the Padé model therefore repeats the result of our previous work,

namely that the Beddington functional response can be derived from an interaction scheme of predators and prey lacking predator interference. However, because of the complicated growth and death terms in eqn (11), the Padé model is much more complicated than the original Beddington model.

Thus, our final simplification step is to assume that C is indeed small compared with $\bar{N}$ and $\bar{P}$, such that

$$\bar{N} - C \approx \bar{N}, \text{ and } \bar{P} - C \approx \bar{P}. \quad (12b, c)$$

Thus, we have to assume that the fraction of predators and prey involved in interaction complexes C is always a small fraction of the total prey densities $\bar{P}$ and the total predator densities $\bar{N}$. Note that for this assumption the Padé approximation should always be allowed. This final simplification step is in fact implicit in our previous paper (Borghans *et al.*, 1996), where the logistic growth of the prey, and the turnover of the predator, were added to the model after the functional response had been calculated. By approximation 12 we finally obtain the Beddington model.

In our previous paper (Borghans *et al.*, 1996) predator interference was always maximal, i.e., $\epsilon = 1$. The same form is provided by our current model when the predator handling time becomes negligible, i.e., for $1/k_3 \rightarrow 0$ [see eqns (7b) and (10h)]. Thus, the current form, i.e., $0 < \epsilon < 1$, is more general, and allows us to tune the importance of the predator interference. For instance, in the absence of interference, i.e., for $\epsilon \rightarrow 0$, the Holling functional response is obtained.

Approximation (12) limits our derivation to predator-prey systems in which complexes are short lived and predation events are rare. Neglecting C in the predator mortality term of eqn (11b) seems acceptable, because it is a more or less arbitrary choice to let the predators in the complex die or not. Additionally, one can compensate for this approximation by adjusting the mortality parameter m . The C terms in the logistic growth of the prey in eqn (11a) pose a more serious problem however. Because of the nonlinear nature of the logistic growth, these terms cannot simply be adjusted for by changing the growth parameters r and K . Neglecting the C term in the logistic growth term, we in fact assume that prey in complex grow just as fast as free prey individuals. Whenever a prey is not aware that a predator has locked-in to it, this could therefore still be a reasonable assumption.

4. Numerical Examples

Whether or not our full model based upon scheme (3), and the various simplification steps that we need

to obtain the minimal model, are of any relevance for predator-prey systems in nature remains an open question, however. Here we approach this question numerically. We have searched the ecological literature for publications estimating the parameter values of predator-prey systems resembling eqn (1). We have found two examples: an algae zooplankton system (Scheffer & De Boer, 1995) and a microtine rodent mustelid predator (Hanski & Korpimäki, 1995). Assuming that these two predator prey systems can be described by our full model of scheme (3) we estimate the unknown parameters k_1 , k_{-1} , k_2 , and k_3 . For the two examples we thus found a full model behavior that seemed to be realistic. Hence scheme (3) can indeed describe the predator-prey interaction.

Next we test the three simplification steps of the full model. Assuming that the behavior of the full model is indeed realistic we study how its behavior is affected by the various simplifications. The results will show that all simplification steps except for the last one hardly affect the model behavior. Therefore, making a minimal model by assuming that the complexes are a small fraction of the total predator-prey densities is the most dubious simplification step.

The ultimate aim of our procedure is to see if our two examples can be fitted to the Beddington model, i.e.,

$$\frac{dN}{dt} = rN(1 - N/K) - \frac{gNP}{h + wP + N}, \quad (13a)$$

$$\frac{dP}{dt} = e \frac{gNP}{h + wP + N} - mP, \quad (13b)$$

where we have defined the lumped parameters as

$$g = \epsilon k_2, \quad h = \epsilon k_m, \quad w = \epsilon, \quad e = c \frac{k_3}{k_3 + m} \simeq c, \quad (13c-f)$$

and where the parameters k_m and ϵ are still defined as

$$k_m = \frac{k_{-1} + k_2}{k_1}, \quad \text{and} \quad \epsilon = \frac{k_3 + m}{k_3 + m + k_2} < 1, \quad (13g, h)$$

and the parameters k_1 , k_{-1} , k_2 , and k_3 are defined by scheme (3). For the ecological systems considered here it natural to assume that the handling time $1/k_3$ should be much shorter than the average life-span of a predator $1/m$. This set a constraint on the realistic values of k_3 and shows that the conversion parameter e in eqn (13f) is approximately the same as the conversion parameter c in scheme (3), i.e., $e \simeq c$. Another constraint is that ϵ cannot equal 0, because this would assume an infinitely high prey capture rate k_2 [see eqn (13h)], which is unrealistic.

Our first numerical example is a Lotka-Volterra Holling type II algae zooplankton model that was

published with realistically estimated parameters (Scheffer & De Boer, 1995). The published parameter estimates are $r = 0.5 \text{ day}^{-1}$, $K = 10 \text{ mg DW l}^{-1}$, $e = 0.6$, $g = 0.4 \text{ day}^{-1}$, $h = 0.6 \text{ mg DW}$, and $m = 0.15 \text{ day}^{-1}$. To test our assumption that this model could have scheme (3) as its underlying interaction scheme, our first job is now to estimate or calculate the unknown parameters k_1 , k_{-1} , k_2 , and k_3 .

Since we require that $k_3 \gg m$, we assume that the handling time of a *Daphnia* is on the order of 1 min, i.e., $k_3 = 1440 \text{ day}^{-1}$. Substituting $k_3 = 1440$, $m = 0.15$, and eqn (13h) into $g = 0.4 = \epsilon k_2$ we compute that $k_2 \approx 0.4$. Hence $\epsilon \approx 1$ and $k_m \approx 0.6$. Assuming that 90% of the prey-predator complexes dissolve because the prey escapes, i.e., assuming that $k_{-1} = 90 k_2 \approx 36.0$, we obtain $k_1 \approx 66.6$. Conversely, assuming that 10% of the complexes dissolve because the prey escapes, i.e., assuming that $k_{-1} \approx 0.004$, we obtain $k_1 \approx 0.67$.

These calculations are quite robust because they change very little when we pick a different value for the handling time. For instance, for $k_3 = 24$, i.e., a handling time of one hour, we obtain virtually indistinguishable values. Even for a handling time of one day we obtain similar values, i.e., $k_2 \approx 0.6$, $\epsilon \approx 0.6$, and $k_m \approx 1$. Thus, fitting scheme (3) to the algae zooplankton parameters we always obtain maximum interference, i.e., $\epsilon \approx 1$.

We numerically test our various simplification steps in Fig. 3 where the behavior and the nullclines of the algae zooplankton model (Scheffer & De Boer, 1995) and of our four models for the same parameters are depicted. The five columns in the Fig. 3 depict the algae-zooplankton, the four-dimensional, the QSS, the Padé, and the minimal model, respectively. In the first row we assume that most of prey in complexes escape, i.e., we set $k_{-1} \approx 36.0 \gg k_2 \approx 0.4$, whereas in the second row most of the prey in complexes are eaten by the predator, i.e., we set $k_{-1} \approx 0.004 \ll k_2 \approx 0.4$.

Figure 3 shows that for these parameters the QSS and the Padé approximation fit the full model and the original Holling model of Scheffer & De Boer (1995) reasonably well. The behavior always remains a limit cycle. Our models may even fit the actual data somewhat better because the algae and zoo-plankton densities are not depleted as much during the troffs of the limit cycle (cf. Scheffer & De Boer, 1995). This is due to the stabilizing effects of the predator interference. The same stabilizing effect is however much too strong in the minimal model where our parameter estimates force us into the limited predation regime with a stable equilibrium. The fact that the minimal model

provides a rather poor fit indicates that for the current parameters too large a fraction of the prey or predators forms complexes, i.e., indicates that eqn (12b) does not hold. The conventional *Daphnia* model can however be considered as a "worst" case for our test because of its large amplitude limit-cycles for both predator and prey (Scheffer & De Boer, 1995), i.e., the complexes are bound to cover too large a fraction of the total number of predators and prey, at least somewhere along the trajectory. It is well known, however, that the conventional model fits the data on oscillating algae and zooplankton densities rather poorly because of these large amplitude limit-cycles (Scheffer and De Boer, 1995). We conclude that for these parameters the minimal model fits the data poorly, but that from the Padé model onwards our models may fit the data better than does the Holling type II model.

4.1. MICROTINE RODENTS AND MUSTELID PREDATORS

Secondly, we applied the same numerical analysis to a parameter setting estimated for microtine rodents (*Microtus*) and mustelid predators (*Mustela nevalis*) (Hanski & Korpimäki, 1995). In this system the prey density is much higher than the predator density, thus C is always small compared with $\bar{N}$. The parameter estimates for this model were $r = 4.05 \text{ year}^{-1}$, $K = 75 \text{ individuals ha}^{-1}$, $e = 0.0023$, $g = 600 \text{ year}^{-1}$, $h = 5.0 \text{ individuals ha}^{-1}$, and $m = 1.0 \text{ year}^{-1}$ (see Appendix A.3 for calculations).

Our estimate for the interference parameter ϵ now depends on the estimate for the handling time. Picking a fast handling time of about one hour, i.e., $k_3 = 8760 \text{ year}^{-1}$, we find $k_2 \approx 644$, $\epsilon \approx 0.93$, and $k_m = 5.4$. Again assuming that 90% of the prey escape, i.e., setting $k_{-1} \approx 57970$ we obtain $k_1 \approx 10929$. Conversely, assuming that only 1% of the prey escape, i.e., setting $k_{-1} \approx 6.5$, we obtain $k_1 \approx 121$. Picking a slow handling time of about 12 hr, i.e., $k_3 = 730$, we obtain $k_2 \approx 3348$, $\epsilon \approx 0.18$, and $k_m = 28$. Thus, for 90% of the prey escaping we find $k_{-1} \approx 301328$ and $k_1 \approx 10920$, whereas for 10% of the prey escaping we find $k_{-1} \approx 37$ and $k_1 \approx 121$.

Figure 4 depicts that for the parameter setting of the Microtine rodent Mustelid predator interaction, the behavior of all our simplified models fits the four-dimensional model and a Holling type II model reasonably well. Hence, we conclude that (i) scheme (3) can apply to this particular system, (ii) our derivation of the minimal model seems justified, and (iii) we can obtain weak and strong predator interference. Our simplifications now work much better because the prey densities are much higher than

the predator densities, i.e., eqn (12b) should always hold.

5. High-Dimensional Models

An essential property of a general functional response is that it is applicable to ecosystems with several (say n) prey species and several (say m) predator species. In order to keep the model as simple as possible such systems are often modeled with a linear functional response (Yodsis, 1989). In this section we show that a generalization to an $n \times m$ system is straightforward for the Holling type II functional response. Unfortunately, predator-dependent functional responses seem to be too complex to allow for such a generalization.

5.1. HOLLING MODEL IN $N \times M$ DIMENSIONS

Following the same derivation scheme as above, the equations for an $n \times m$ dimensional system with Holling type II functional response can be derived by writing down the $n \times m$ dimensional form of eqns (5), where k_2 is replaced by α_{ij} :

$$\frac{dN_i}{dt} = rN_i \left(1 - \frac{N_i}{K}\right) - N_i \sum_j P_j \alpha_{ij}, \quad (14a)$$

$$\frac{dP_i}{dt} = -mP_i + (1+c)k_3 \sum_j H_{ij} - P_i \sum_j N_j \alpha_{ji}, \quad (14b)$$

$$\frac{dH_{ij}}{dt} = \alpha_{ij}P_iN_j - mH_{ij} - k_3H_{ij} = 0. \quad (14c)$$

We define total predators as

$$\bar{P}_i \equiv P_i + \sum_j H_{ij}, \text{ and obtained}$$

$$\frac{d\bar{P}_i}{dt} = -m\bar{P}_i + c \sum_j k_3 H_{ij}. \quad (15a, b)$$

Solving (14c) for H_{ij} and substituting the result in (15a) yields

$$P_i = \frac{(m+k_3)\bar{P}_i}{(m+k_3) + \sum_j \alpha_{ij}N_j}. \quad (16)$$

For the general predator prey model we thus obtain

$$\frac{dN_i}{dt} = rN_i \left(1 - \frac{N_i}{K}\right) - (m+k_3) \sum_j \frac{\alpha_{ij}N_i\bar{P}_j}{(m+k_3) + \sum_l \alpha_{il}N_l}, \quad (17a)$$

$$\frac{d\bar{P}_i}{dt} = -m\bar{P}_i + ck_3 \sum_j \frac{\alpha_{ij}\bar{P}_iN_j}{(m+k_3) + \sum_l \alpha_{il}N_l}, \quad (17b)$$

where the $\sum_j$ means that for each predator each prey species functions as an independent resource, and the $\sum_l$ term weights the availability of this resource by the "time" this predator spends at all other resources.

5.2. PREDATOR DEPENDENT MODEL IN $N \times M$ DIMENSIONS

Models with a predator dependent functional response are more complex and much more difficult to generalize to higher dimensional systems. De Boer & Perelson (1995) propose a generalization to an $n \times 1$ system in a similar model describing T-lymphocyte proliferation. Following their approach the Padé approximation for C in a system with one predator and n prey species becomes:

$$C_i \approx \frac{\epsilon \bar{N}_i \bar{P}}{\epsilon k_{m_i} + \epsilon \bar{P} + \sum_j \bar{N}_j \frac{\bar{P} + k_{m_i}}{\bar{P} + k_{m_j}}}, \quad \text{where } \epsilon = \frac{k_3 + m}{k_3 + m + \sum_j k_{2j}}, \quad (18a, b)$$

which is unfortunately too complicated for a minimal model.

For systems with n predator and n prey species a generalization is not possible at all (De Boer & Perelson, 1995). As we prefer to have models which can be applied generally, we here pinpoint a major disadvantage of the Beddington functional response. Thus, we definitely pay a price for having a predator-dependent functional response.

6. Discussion

Our approach, which uses reaction schemes and quasi-steady-state assumptions for the formal derivation of a functional response, has given us a clear mechanistic argument for the Beddington functional response. This fulfils our first requirement for a good functional response. The requirement of general applicability is however not fulfilled because the Beddington functional response cannot be generalized to systems of several interacting prey and predator species. Thus, for two-dimensional systems of one prey and one predator species the Beddington functional response seems an elegant choice, because it allows for higher stability and for the Paradox of Enrichment.

Our numerical tests show that the behavior of the quasi-steady-state model and the Padé model is normally a good approximation of the behavior of the four-dimensional model. The most critical simplification step is to ignore the complexes of predator and prey in the logistic growth term. This point was missed in our previous analysis (Borghans *et al.*, 1996). An important issue now is therefore the growth of the prey in complex, i.e., those prey individuals on which predators have locked-in. Prey individuals that are being chased by a predator are indeed unlikely to contribute to the growth of the prey population. The individual algae that a zooplankton individual is trying to catch are, however, probably unaware of being in the field of attention of a predator, and will therefore continue to contribute to population growth. Then, our derivation simplifies because the growth term of the prey can be added on to the quasi-steady-state model [as was done previously (Borghans *et al.*, 1996)].

One can think of several ecological explanations for our complex of predator and prey. The only general restriction is that the interaction complex should not necessarily result in the death of the prey. The functional response we obtain from the various reaction schemes depends on our definition of total numbers of prey and total numbers of predators. Mathematically one can still derive the Beddington functional response from scheme (3) if the complex is not allowed to fall apart into predator and prey (i.e. $k_{-1} = 0$). Sticking to our original definition of total numbers of prey [eqn (10a)], one obtains the same functional response because the only effect of k_{-1} in eqn (11) is a quantitative influence on the value of k_h . In an ecological context however, it is not arbitrary how one defines the total numbers of prey (i.e. our variable $\bar{N}$). If k_{-1} equals zero the prey in complex are dead, and hence should no longer contribute to the total numbers of prey. Excluding the prey in complex from the total prey numbers (i.e. define $\bar{N} \equiv N$) we obtain a normal (Holling type II) functional response. Thus the Beddington functional response can only be derived from scheme (3) if we interpret the predator prey complex as an interaction where the prey can still escape from.

Elsewhere we provide an alternative approach for deriving a predator-dependent functional response. This other approach focuses on situations where the prey is unaware of being in the field of attention of the predator. One visualization of this is a prey species that is distributed randomly over a certain area. The predators defend a territory within this area, and interact with the prey within their territory only. The territory size has a maximum when the predator

density is low, and declines when the predator density increases. The latter is responsible for the predator interference. Depending on the form of the (monotonically decreasing) function describing the relation between the territory size and the predator density we obtain (i) the ratio-dependent model, (ii) the Beddington model, or (iii) a functional response with quadratic predator interference (Huisman & De Boer, in preparation). Again we find that the ratio-dependent model is obtained when we pick unrealistic functions, i.e., those that allow for infinite territory sizes at low predator densities.

The numerical analysis of the Microtine rodents Mustelids parameters shows that the behavior of our models is almost identical to that of the Holling type II model. This is due to the high difference in the abundance of predator and prey, which ensures that the number of complexes is always a small fraction of the total prey population. This confirms the prediction in our previous paper (Borghans *et al.*, 1996), namely that for $N \gg P$ the Beddington functional response can be approximated by a Holling type II functional response.

The Beddington functional response is definitely superior to the ratio-dependent model. It can be derived from clear mechanistic reasoning and it lacks the strange behavior at low predator and prey concentrations. All of the advantages of the ratio-dependent models claimed by Arditi & Ginzburg (1989) also holds for the Beddington model. Additionally the Beddington functional response can be regarded as a generalization of the Holling type II function. Unfortunately the Beddington functional response cannot be generalized to high-dimensional systems with many prey and predator species. Thus, we pay a price for predator interference, and in high-dimensional systems the Holling type II function remains the superior functional response.

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APPENDIX

A.1. Stability of the Ratio-dependent Model

The ratio-dependent model (Arditi & Ginzburg, 1989) cannot account for the Paradox of Enrichment. We here prove that the non-trivial equilibrium point

of the ratio-dependent model (Arditi & Ginzburg, 1989), i.e.,

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - \frac{bNP}{hP + N}, \quad (\text{A.1})$$

$$\frac{dP}{dt} = \frac{cbNP}{hP + N} - mP, \quad (\text{A.2})$$

cannot be destabilized by increasing the carrying capacity K only. The equations for the nullclines of the prey and predator are

$$P = \frac{aKN - aN^2}{aKh - ahN - bK}, \quad \text{and} \quad (\text{A.3})$$

$$P = \frac{cbN - mN}{mh}, \quad (\text{A.4})$$

respectively. Thus the non-trivial equilibrium point is found at

$$N = K \left(1 - \frac{b}{ah} + \frac{m}{cah} \right). \quad (\text{A.5})$$

The stability of the equilibrium point is determined by the relative positions of the top of the humped prey isocline and this equilibrium point. The position of the top is found where the derivative of the prey isocline [eqn (A.3)] with respect to N equals zero. Thus, the top is located at

$$N = K \left(\frac{ah + b \pm \sqrt{b(b - ah)}}{ah} \right). \quad (\text{A.6})$$

As both the top [eqn (A.6)] and the equilibrium point [eqn (A.5)] change proportional to K , a stable system can never be destabilized by increasing K only.

A.2. Positive root of C

Equation (10f) can be written as

$$C = \frac{1}{2}(\bar{P}\epsilon + \bar{N} + k_m\epsilon \pm \sqrt{(\bar{N} - \bar{P}\epsilon)^2 + \epsilon k_m(2\bar{P}\epsilon + k_m\epsilon + 2\bar{N})}). \quad (\text{A.7})$$

The square-root term is thus larger than

$$\sqrt{(\bar{N} - \bar{P}\epsilon)^2} = \bar{N} - \bar{P}\epsilon. \quad (\text{A.8})$$

Thus, for the positive root of eqn (A.7) we obtain

$$C \geq \bar{N} + \frac{k_m\epsilon}{2}, \quad (\text{A.9})$$

which violates the condition $C \leq \bar{N}$ that follows from the conservation law. Thus, only the negative root of eqn (10f) is valid.

A.3. Parameter Derivation for the Microtine Model

The parameters used in the Microtine rodent Mustelid model are derived from a more complicated model used by Hanski & Korpimäki (1995). These authors used two different models for summer ($\dot{N}_1, \dot{P}_1$) and winter ($\dot{N}_2, \dot{P}_3$), and a third model for low prey density ($\dot{P}_2$). These basic models are

$$\dot{N}_1 = rN \left(1 - \frac{N}{K}\right) - \frac{cPN}{N+D}, \quad (\text{A.10})$$

$$\dot{P}_1 = vP \left(1 - \frac{qP}{N}\right), \quad (\text{A.11})$$

$$\dot{N}_2 = r'N \left(1 - \frac{N}{K'}\right) - \frac{cPN}{N+D}, \quad (\text{A.12})$$

$$\dot{P}_2 = -d_{\text{high}}P, \quad (\text{A.13})$$

$$\dot{P}_3 = -d_{\text{low}}P, \quad (\text{A.14})$$

and they are joined to one model in

$$\frac{dN}{dt} = \Omega \dot{N}_1 + (1 - \Omega) \dot{N}_2, \quad (\text{A.15})$$

$$\begin{aligned} \frac{dP}{dt} = & \Omega(\dot{P}_2 + \Delta(\dot{P}_1 - \dot{P}_2)) \\ & + (1 - \Omega)(\dot{P}_2 + \Delta(\dot{P}_3 - \dot{P}_2)), \end{aligned} \quad (\text{A.16})$$

where Ω is a sinusoidal function of time and describes the seasonal fluctuation. Δ is a smooth switching function of the prey density that is on whenever the prey density is above a critical value.

Hanski & Korpimäki (1995) provide estimates for all parameters of this model. Here we employ these parameter values for estimating the parameters of a corresponding Holling type II model. Some parameters in the Holling type II model (i.e., r, K, g, h) have exact counterparts in the seasonal model (i.e., r, K, c, D). For these parameters we simply took the average of the summer and winter values, or the average of a range used in the seasonal model. The estimates found were $r = 4.05 \text{ year}^{-1}$, $K = 75$ individuals ha^{-1} , $g = 600 \text{ year}^{-1}$, $h = 5$ individuals ha^{-1} .

The conversion factor for the two trophic levels (e) was not defined in the seasonal model. We therefore calculated it by dividing the intrinsic growth rate of the predator (v) in eqn (A.11) by the prey capture rate. This value was divided by two because winter growth rate is zero. This yielded $e = 0.0023$, and will slightly overestimate the conversion factor, because summer mortality is included in the intrinsic growth rate.

The seasonal model has two different mortality rates for the predator, i.e., $d_{\text{low}} = 0.1$ for high prey densities, and $d_{\text{high}} = 5$ for low prey densities. We took an arbitrary value between d_{low} and d_{high} . Our estimate lies closer to d_{low} because most of the time the system is in the region where d_{low} is valid. Thus we picked $m = 1.0 \text{ year}^{-1}$ as a reasonable estimate.