Testing for predator dependence in predator–prey dynamics: a non-parametric approach

Christian Jost[1]* and Stephen P. Ellner[2]

[1]*Institut National Agonomique Paris-Grignon, Ecologie des Populations et Communautés, 16 rue Claude Bernard, 75231 Paris Cedex 05, France*

[2]*Biomathematics Graduate Program, Department of Statistics, North Carolina State University, Raleigh, NC 27695-8203, USA*

The functional response is a key element in all predator–prey interactions. Although functional responses are traditionally modelled as being a function of prey density only, evidence is accumulating that predator density also has an important effect. However, much of the evidence comes from artificial experimental arenas under conditions not necessarily representative of the natural system, and neglecting the temporal dynamics of the organism (in particular the effects of prey depletion on the estimated functional response). Here we present a method that removes these limitations by reconstructing the functional response non-parametrically from predator–prey time-series data. This method is applied to data on a protozoan predator–prey interaction, and we obtain significant evidence of predator dependence in the functional response. A crucial element in this analysis is to include time-lags in the prey and predator reproduction rates, and we show that these delays improve the fit of the model significantly. Finally, we compare the non-parametrically reconstructed functional response to parametric forms, and suggest that a modified version of the Hassell–Varley predator interference model provides a simple and flexible function for theoretical investigation and applied modelling.

Keywords: functional response; prey dependence; predator dependence; ratio dependence; non-parametric reconstruction; predator–prey

1. INTRODUCTION

The recent debates about ratio-dependent predation (e.g. Abrams 1994; Sarnelle 1994; Akçakaya *et al.* 1995; Berryman *et al.* 1995; Abrams 1997; Bohannan & Lenski 1999; Abrams & Ginzburg 2000) have drawn ecologists' attention to the issue of correctly specifying the functional response (the instantaneous rate of prey consumption per predator). As the link between predator and prey dynamics, the functional response is necessarily critical for predator–prey interactions, and it is also important for the dynamics of complex food webs such as the response of lakes or soil macrofauna to nutrient enrichment (e.g. McCauley *et al.* 1988; Arditi *et al.* 1991*a*; Ponsard *et al.* 2000). The choice of a particular functional form to model a process rate can have surprising effects on statistical inference and prediction (e.g. Yodzis 1994; Wood & Thomas 1999).

Functional response equations that are strictly prey dependent, such as the Holling family, are predominant in the literature. The term 'prey dependent' means that the consumption rate by each single predator is only a function of prey density, and a 'predator-dependent' functional response is one in which both predator and prey densities affect the per-predator consumption rate (Arditi & Ginzburg 1989). One talks of 'ratio dependence' when consumption is a function of the ratio prey to predator density. Theoretical studies have shown that the dynamics of models with predator-dependent functional responses can differ considerably from the dynamics of correspondingly structured models with prey-dependent functional responses (Rogers & Hassell 1974; DeAngelis *et al.* 1975; Arditi & Ginzburg 1989; Kuang & Beretta 1998; Jost *et al.* 1999).

Although the strictly ratio-dependent model has attracted considerable attention (and emotion), the consumption process is potentially influenced by so many factors (prey and predator densities, stochastic or periodic environmental factors, metabolic by-products in cultures, etc.) that it is unlikely that one mathematical expression can describe the functional response in all systems. Thus, the key issue with regard to quantifying the functional response is not ratio dependence, but the potential importance of predator dependence: How commonly does it occur, and is it sufficiently weak that we can safely ignore it? Several recent empirical studies of this question (Arditi & Akçakaya 1990; Arditi *et al.* 1991*b*; Dolman 1995; McCarthy *et al.* 1995; Skalski & Gilliam 2000; Ponsard *et al.* 2000; Jost & Arditi 2000*b*; see also review in Sutherland 1996) show that predator dependence in the functional response is very frequent in laboratory and natural systems.

Although these empirical studies have provided support for the concept of predator dependence, this support is qualified by some significant limitations. Many of these studies are based on arena experiments that, in order to achieve replication among subjects, often involve 'starved' predators (deprived of food for an extended period before the experiment). The feeding behaviour of 'starved' predators might be atypical or of limited relevance to the field. In addition, processes occurring on different time-scales in the field (e.g. behavioural scale versus demographic scale) can lead to indirect predator dependence that is undetectable in an arena experiment (Michalski *et al.* 1997; Poggiale *et al.* 1998). Subsidiary problems with many arena studies are small sample size, in the sense that the design involved a small number of (prey, predator) density combinations, and that data analyses often do not account for the potential effects of

*Author for correspondence (christian.jost@inapg.inra.fr).

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prey depletion during the experiments. Because higher predator density will increase prey depletion during the course of the experiment, prey depletion effects can create spurious apparent predator dependence (Arditi 1982; Arditi & Saïah 1992). Some other studies with data from field observations have mostly been based on changes in equilibrium or mean abundances over a gradient of enrichment (e.g. Arditi *et al*. 1991*b*; McCarthy *et al*. 1995; Ponsard *et al*. 2000). The assumption of the systems being at equilibrium is often difficult to validate in a seasonal environment, and the data analyses have typically been framed as a contest between conventional prey-dependent models and the ratio-dependent model.

A second and more general problem is that comparisons have typically involved comparing specific prey-dependent equation(s) with specific predator-dependent equation(s), rather than contrasting the two qualitative assumptions. Given that there are over 20 proposed equations for the functional response (collections in May (1976) and Michalski *et al*. (1997)), one rarely finds a comprehensive comparison rather than a selection between a few preferred equations. The outcome of such a comparison may be sensitive to the selection of contesting models, with the particular risk of incorrectly rejecting prey dependence in favour of predator dependence due to a poor choice of the parametric equation to represent the hypothesis of prey dependence.

Here we present a study that avoids these limitations. We use as data time-series of predator–prey dynamics over multiple generations, and a non-parametric approach that minimizes the confounding effects of the choice of functional forms. Our study has its own weaknesses, due to the problems of inferring feeding rates indirectly from the resulting population dynamics, and in particular the need to assume a 'general' model of the population dynamics to estimate the functional response. Although the key assumptions of our model are supported by the data (as discussed in § 3), the limitations of the data mean that we cannot have total confidence in the population model. However, these problems are completely different from the problems of previous studies, so we interpret our results as a useful complement to previous work. As a by-product, our approach allows us to test the hypothesis of conservation of mass (rather than assuming it through theoretical arguments) and whether a delay between consumption and reproduction (for both prey and predator) improves agreement between model and data significantly.

The data come from a protozoan experiment (Veilleux 1976) with *Paramecium aurelia* as prey and *Didinium nasutum* as predator, and are time-series of twice-daily counts of predator and prey abundance over several sustained population cycles. These are the same organisms as in the classical work on predator–prey systems of Gause (1935) and that of Luckinbill (1973). Our goal in analysing these data is to extract qualitative information about the functional response, rather than trying to identify the 'true' functional response equation. We would like to distinguish between prey dependence, ratio dependence and more general predator dependence in the functional response, but we do not attempt to identify a specific 'best-fitting' functional response equation.

Our analysis uses the approach developed by Ellner *et al*. (1997). The basic structure of the model is derived from biological considerations and data independent of the time-series data used to fit the model, and the functional response is estimated non-parametrically, yielding a 'semimechanistic' predator–prey model. In the context of function estimation 'non-parametric' does not mean 'distribution free' (which is the sense of non-parametric in, for example, 'non-parametric correlation coefficient'). It means that the shape of the function (in our case, the functional response) is estimated from a high- (and potentially infinite) dimensional space of functions, rather than choosing the (few) parameters of a particular functional form with limited flexibility.

As in Ellner *et al*. (1997), the model is fitted by gradient matching: the time-series are smoothed to obtain an estimate of the instantaneous rates of population change (the 'gradient' of population density), and the model can then be fitted by weighted least-squares regression. The procedure for gradient estimation that we use here (described briefly in electronic Appendix A available on The Royal Society Web site) is one developed by Ellner & Seifu (2000). Getting accurate gradient estimates is only possible if the time-series are sampled frequently enough relative to the natural time-scale of system dynamics, and if measurements are sufficiently accurate. Simulation studies reported in § 4(*a*) indicate that gradient estimates for the data analysed here will be quite accurate.

We begin with a review of the data, and then present the general model that is the basis for our analyses. The statistical methods used to fit and test the non-parametric functional response equations are outlined in § 4. In the text we present the main ideas, and technical details are deferred to a series of electronic appendices available on The Royal Society Web site.

2. THE DATA

The protozoan predator–prey system of *P. aurelia* and *D. nasutum* is a classic in population ecology (Gause 1935; Luckinbill 1973; Salt 1974). However, only Veilleux (1976, 1979) refined the previous techniques sufficiently to obtain sustained coexistence with regular predator–prey cycles. *Paramecium* was grown on Cerophyl medium (which acts as a bacterial nutrient and supports the vigorous bacterial populations upon which the *Paramecium* feed) in varying concentrations (denoted by CC*x*, see Veilleux (1976) p. 24; CC $1.0 \approx 1.8$ g l^{-1}). Varying the Cerophyl concentration corresponds to varying the prey carrying capacity and the growth rate (see Veilleux (1976) fig. 2*a*–*d*). Methyl cellulose was added to thicken the medium, thus slowing down predator and prey movement. Protozoan abundance was measured by non-destructive counting (each point represents the mean of eight countings). Measurements were taken every 12 h and the experiments were run for 25–35 days.

Cycling coexistence was obtained in this methyl cellulose medium for Cerophyl concentrations ranging from CC 0.375 to 0.5. For higher Cerophyl concentrations, extinction occurred after two to three oscillations. For lower concentrations the predator went extinct, sometimes after depleting the prey to extinction.

Here we analyse the three longest time-series that were reported in Veilleux (1976), which are shown in figure 1
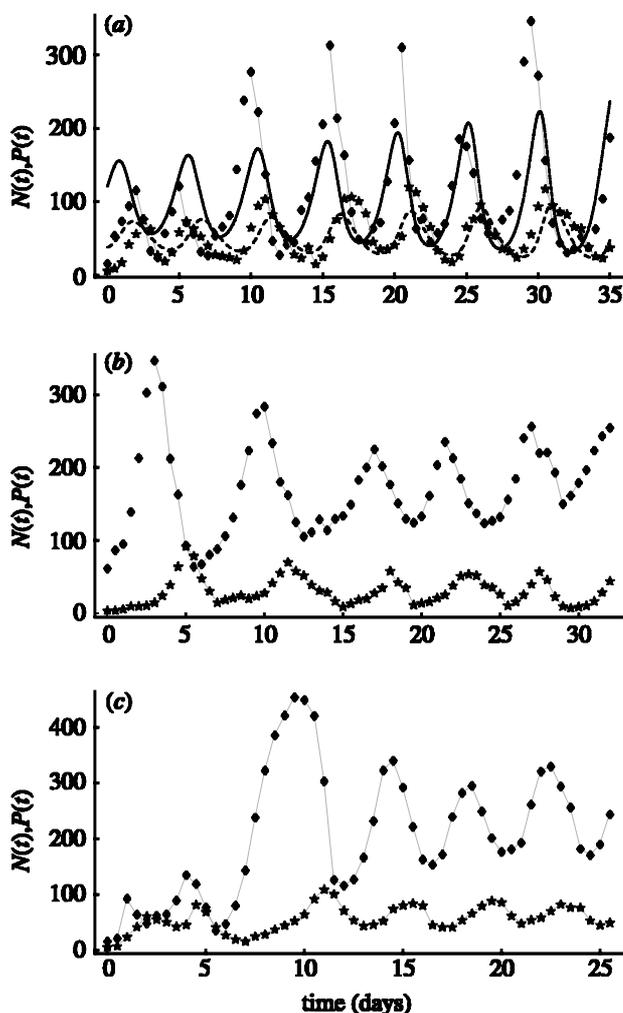
Figure 1. Original predator–prey data with the Cerophyl concentrations under which they were run (time measured in days). Diamonds are the prey measurements and stars the predator abundances. (*a*) Data set 11a, CC 0.5; (*b*) data set 12a, CC 0.375; (*c*) data set 14c, CC 0.5. (*c*) From an experiment with artificial predation on predators. The straight and dashed lines in the first panel are the fitted trajectories of the prey and predator populations for a model with logistic growth and a DeAngelis–Beddington type functional response with estimated parameters $r = 2.0$, $K = 6620$, $a = 0.045$, $h = 0.021$, $c = 0.0016$, $e = 0.284$ and $\mu = 1.06$ (see §4(a) for details on the fitting procedure).

(recovered by scanning and digitizing figs 11*a*, 12*a* and 14*c* in Veilleux (1976)). For each predator–prey time-series there is a corresponding experiment, under the same conditions, of the prey cultured in isolation (fig. 2*b*,*c* in Veilleux (1976) shown on our fig. 2*a*,*e*). Throughout this paper we will call these time-series by the number of the figure from which they were retrieved, i.e. 11a, 12a, 14c, 2b and 2c. B. G. Veilleux (personal communication) was not able to provide the original data of these experiments.

(a) *Sampling errors*

Fitting models to these data requires a goodness-of-fit criterion. Veilleux's efforts to quantify his sampling errors provide information that can be used to construct a weighted least-squares criterion. The errors in these counts were summarized by Veilleux (1976) table 1. As

observed by Veilleux, the error variance is clearly not constant. However, we have found that they conform to the expectation for random (Poisson) population subsampling that the standard deviations for prey and predator, σ_N and σ_P, are proportional to the square root of abundance, $\sigma_N = 0.417\sqrt{N}$ and $\sigma_P = 0.165\sqrt{P}$, with multiple $r^2 > 0.95$ (N and P stand for prey and predator abundance, respectively, measured as individuals per millilitre). The resulting goodness-of-fit criterion is therefore

$$E = \sum_{i=1}^{q} \frac{(n_i - \hat{n}_i)^2}{0.417^2 n_i} + \sum_{i=1}^{q} \frac{(p_i - \hat{p}_i)^2}{0.165^2 p_i}, \tag{1}$$

where n_i and p_i are the observations of prey and predator abundance at time t_i, and $\hat{n}_i$ and $\hat{p}_i$ are the corresponding model-predicted values.

3. THE GENERAL MODEL STRUCTURE

Our analysis of the data is based on a general model for interactions between unstructured prey and predator populations with overlapping generations:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = Nf(N_\delta) - g(N, P)P, \tag{2a}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = eg(N_\tau, P_\tau)P - \mu P, \tag{2b}$$

with prey density N, predator density P, prey growth rate $f(N)$, functional response $g(N, P)$, conversion efficiency e and predator mortality rate μ. Here N (for example) is a shorthand for the time-dependent variable $N(t)$. The subscripts τ and δ refer to time-delays, e.g. N_τ denotes $N(t - \tau)$. Two particular features of this model require some comment and justification: the time-delays, and the assumption of a linear conversion efficiency between prey consumption and predator reproduction.

Time-delays have been proposed at several places in system (2), which may have a variety of effects on stability for this system (e.g. Wangersky & Cunningham 1957; Goel *et al.* 1971; Cushing 1977; Gurney *et al.* 1980; Blythe *et al.* 1982; Hastings 1983; Zhao *et al.* 1997; Beretta & Kuang 1998). In equations (2) we allow for a time-delay between consumption and reproduction in both prey (δ) and predator (τ) individuals. The values of these delays are estimated from the experimental data. Because reproduction is by fission, new offspring are immediately counted as members of the population (i.e. there is no 'immature class'), and the state variables in the model are total numbers of individuals of all ages. The delay should thus act on the fission rates, while the non-delayed values of N and P in equations (2) represent the fact that fission events 'now', by individuals alive 'now', create new individuals who are immediately available for census.

The data on prey cultured in isolation make it possible to estimate the form of the prey-growth function f, and to estimate the time-delay δ. Figure 2 illustrates the process for the analysed experimental conditions. The prey growth curve 2*b* from Veilleux (1976) (our figure 2*a*) with CC 0.5 (corresponding to series 11a and 14c) exhibits overshoot of the apparent 'carrying capacity', which argues for the existence of a delay. The same also occurs, though the effect is less pronounced, in the other experimental condition with CC 0.375 (series 2c in figure 2*e*). In
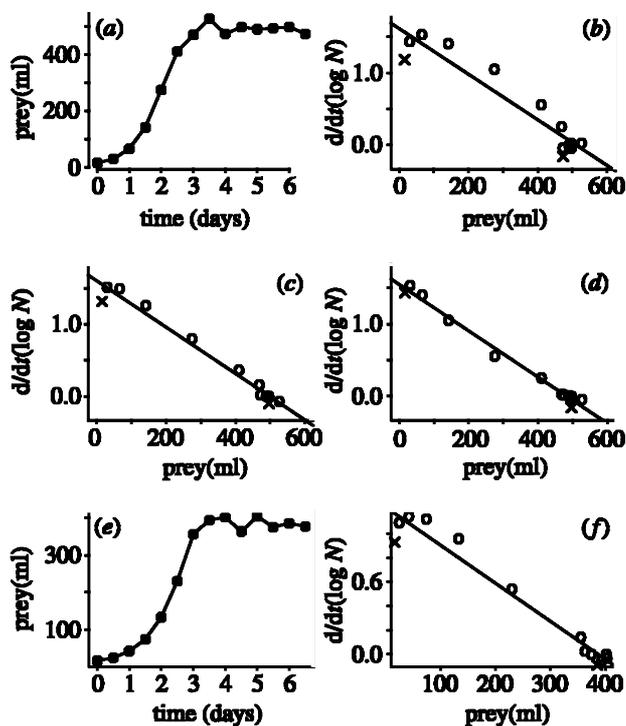
Figure 2. Prey-growth data in the absence of predators (time measured in days) and how they were used to estimate the parameters of the prey-growth function $f(\mathcal{N}_\delta) = r(1 - \mathcal{N}_\delta/K)$. See text for details. (*a–d*) analysis of series 2b with CC 0.5, (*a*) raw data, (*b*) no delay, (*c*) delay = 6 h, (*d*) delay = 12 h; (*e–f*) analysis of series 2c with CC 0.375, (*e*) raw data, (*f*) delay = 12 h. The points marked with a cross are the beginning and end-points of the time-series where the gradient estimate is less precise.

the absence of predators, the prey equation becomes $d\mathcal{N}/dt = \mathcal{N}f(\mathcal{N}_\delta)$ and therefore $d(\log\mathcal{N})/dt = f(\mathcal{N}_\delta)$. Smoothing the time-series of $\log\mathcal{N}$ by the methods described in electronic Appendix A provides an estimate of $d(\log\mathcal{N})/dt$, which is plotted against $\mathcal{N}_\delta$ for different values of δ (figure 2*b–d*). For δ near zero, the plot produces the appearance of an Allee effect, for which there is no mechanistic basis in the system (no need to find mates, for example). Increasing the delay to 12 h produces a linear relationship (logistic growth: $f(\mathcal{N}_\delta) = r(1 - \mathcal{N}_\delta/K)$), and we therefore use $\delta = 12$ h. The same time-delay also produces a decent fit for the other experimental conditions analysing series 2c (figure 2*f*) with CC 0.375 (corresponding to series 12a). Note that this process also gives estimates of r and K that will be used in the analysis of the longer time-series with coexisting prey and predator. Veilleux (1976, table 3*a*) measured the number of divisions per day for the *Paramecium*. These give an approximate idea of the generation time which should correspond to the length of the delay. His estimate of 9–15 h corresponds well with our choice of 12 h. Within this range of biologically plausible values for δ, any improvement in accuracy that could be achieved by estimating more precisely an 'optimal' value of δ would be more than outweighed by the errors introduced by the need to interpolate the data to a higher sampling frequency. We therefore treat $\delta = 12$ h as a known parameter in all subsequent analyses.
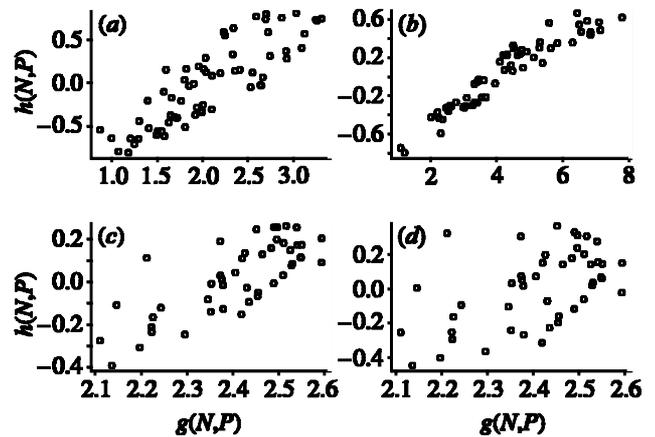

Figure 3. The functional response ($g(\mathcal{N}, P)$) plotted against the predator reproductive rate ($h(\mathcal{N}, P)$) as reconstructed from the prey and the predator equation separately to test the conservation of mass hypothesis, $h(\mathcal{N}, P) = eg(\mathcal{N}, P) - \mu$. See electronic Appendix B for details. (*a*) Series 11a, $\tau = 0.3$ days; (*b*) series 12a, $\tau = 0.6$ days; (*c*) series 14c, $\tau = 0.1$ days; (*d*) series 14c, $\tau = 0.3$ days.

Theoretical arguments for the use of conservation of mass were developped by Ginzburg (1998). Here we can go a step further by testing this assumption and the linear conversion between consumption and reproduction. The prey consumption rate can be estimated from the prey equation alone, while the predator reproductive rate can be estimated from the predator equation alone. Electronic Appendix B details how to use this idea to visualize the relationship between consumption of prey and predator reproduction (see figure 3), and we conclude that the relationship appears to be linear, at least within the accuracy of the data.

4. GENERAL METHODS TO FIT AND COMPARE MODELS

After these preliminary analyses we can reconstruct and compare the functional response models.

(a) *Reliability of gradient estimation*

The method to estimate the population gradient (electronic Appendix A) requires that the data are sampled sufficiently frequently and with not too much error in order to give reliable estimates. We therefore have to test if our data (figure 1) fulfill these requirements. This was done by parameterizing equations (2) with a (non-delayed) logistic prey-growth function and a (non-delayed) DeAngelis–Beddington type functional response (see table 1) and then fitting this model by standard trajectory fitting to data set 11a. This trajectory fitting is described in detail in Harrison (1995) and consists of integrating numerically the solutions of the differential equation system (i.e. the trajectories), computing the error with equation (1) and then finding parameter values that minimize this error. Figure 1*a* shows the resulting trajectories of prey and predator. This fitted trajectory was then sampled at 12 h intervals (similar to the real experiments), adding an observation error similar to that in Veilleux's data (Veilleux 1976, table 1). For this artificial time-series the known gradient can now be compared (graphically

Table 1. *Fitting different functional response models to Veilleux's data sets 11a, 12a and 14c* [a]

(WSSR, weighted sum of squared residuals.)

model	$g(N, P)$	11a		12a		14c	
		WSSR	τ	WSSR	τ	WSSR	τ
Lotka–Volterra, Holling type I	aN	470	0.0	278	0.32	292	0.0
Holling type II	$\dfrac{aN}{1 + ahN}$	428	0.0	274	0.30	248	0.0
Holling type III	$\dfrac{aN^2}{1 + ahN^2}$	447	0.0	277	0.29	267	0.0
Ivlev	$a(1 - e^{-cN})$	428	0.0	274	0.30	254	0.0
ratio-dependent II	$\dfrac{aN}{P + ahN}$	**393**	0.38	**178**	0.83	**187**	0.40
ratio-dependent III	$\dfrac{aN^2}{P^2 + ahN^2}$	473	0.36	200	0.80	207	0.40
Hassell–Varley type I	aNP^{-m}	447	0.23	214	0.76	289	0.20
Holling–Tanner		517	0.42	258	0.77	198	0.40
Hassell–Varley type II	$\dfrac{aN}{P^m + ahN}$	**382**	0.30	178	0.83	**125**	0.62
DeAngelis–Beddington	$\dfrac{aN}{1 + ahN + cP}$	392	0.32	177	0.82	187	0.40
Crowley–Martin	$\dfrac{aN}{(1 + ahN)(1 + cP)}$	392	0.30	**175**	0.92	179	0.47
Watts	$a(1 - e^{-cN/P^m})$	386	0.30	177	0.81	146	0.55
Leslie–Beddington		517	0.42	247	0.77	198	0.40

[a] The numbers are goodness-of-fit (equation (3)) and the estimated delay τ. The horizontal lines separate functions with different numbers of parameters and predator–prey systems that have no conservation of mass (Holling–Tanner and Leslie–Beddington). The best fits amongst equally complex models are emphasized.

and by linear regression) with the estimated gradient. Even with noise in the data these estimates are sufficiently accurate for our needs ($r^2 > 0.99$).

(b) *Fitting parametric functional response equations*

For comparison to the non-parametric estimates, we will fit also a couple of parametric functional response models. These models include the well known (prey-dependent) Holling type I, II and III family, their equivalents in the ratio-dependent approach, Ivlev's (1961) function and some more complex models such as the DeAngelis–Beddington and the type II Hassell–Varley functional responses, Crowley & Martin's (1989) pre-emption model and Watt's (1959) function which is the predator-dependent extension of Ivlev's function (see table 1 for formulae). We also added two predator–prey models that do not have conservation of mass: the well-known Holling–Tanner (or Leslie–May) model (Tanner 1975) and a variant of this model where the Holling type

II functional response is replaced by the DeAngelis–Beddington type functional response (see table 1). With the functional response specified parametrically and the gradients estimated separately, fitting the differential equation model (equations (2), with logistic prey growth and r, K and δ as estimated in §3) to the data becomes as simple as fitting a discrete model, a standard nonlinear optimization problem. By a Taylor expansion argument we can consider the gradient to have an observation error that is proportional to the corresponding abundance estimate. The resulting goodness-of-fit criterion, adapted from equation (1), is therefore the weighted sum of squared residuals

$$\text{WSSR} = \sum_{i=1}^{q} \frac{(x_i - \hat{x}_i)^2}{0.417^2 n_i} + \sum_{i=1}^{q} \frac{(y_i - \hat{y}_i)^2}{0.165^2 p_i}, \qquad (3)$$

where x_i and y_i are the estimates of the gradient of prey and predator at time t_i, and $\hat{x}_i$ and $\hat{y}_i$ are the

corresponding model-predicted values. For the actual regression we used the standard downhill simplex method of Nelder and Mead, combined with simulated annealing (routine amotsa from Press *et al.* (1992), implemented in C++). For all fits we used multiple initial parameter estimates, to confirm that best-fitting parameters were well identified. The artificial data described in the previous paragraph will also be fitted by these parametric models to test whether detailed model selection is feasible.

(c) *Non-parametric reconstruction of the functional response*

The non-parametric fitting techniques used in §3 to test the conservation of mass hypothesis (details in electronic Appendix B) reconstructed prey consumption and predator reproduction as functions of two independent arguments $\mathcal{N}$ and P, but they often collapsed into their 'null space' (the simplest possible model in the particular model family). This indicates that the reconstructed general functions, while they served well to validate the conservation of mass hypothesis, might not be reliable enough to perform model selection. We therefore limit ourselves to models in which g is a function of a single argument, $g = g(z)$, with $z = \mathcal{N}$ (prey dependence), $z = \mathcal{N}/P$ (ratio dependence) or $z = \mathcal{N}/P^m$ (which we will call a generalized Hassell–Varley functional response). In the last case, m is estimated along with the other nonlinear parameters in the model. Imposing this restriction could potentially make it harder to detect significant predator dependence.

After rearranging equations (2),

$$\frac{\mathrm{d}\mathcal{N}}{\mathrm{d}t} - r(1 - \mathcal{N}_\delta/K)\mathcal{N} = -\hat{g}(z)P, \tag{4a}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = e\hat{g}(z_\tau)P - \mu P, \tag{4b}$$

with $z = \mathcal{N}$, $z = \mathcal{N}/P$ or $z = \mathcal{N}/P^m$, $\hat{g}(z)$ will be approximated by penalized regression splines (Eilers & Marx 1996; Ruppert & Carroll 1997; Ruppert & Carroll 2000). This is a fixed knot spline with knots $0 < \nu_1 < \ldots < \nu_m < B$, where $B = \max_{1 \leq i \leq q} (z_i)$ (q being the length of the time-series) and the fitted spline estimate $\hat{g}(z)$ can be written as

$$\hat{g}(z) = \sum_{j=0}^{d} \beta_j z^j + \sum_{j=1}^{m} \beta_{j+d} (z - \nu_j)_+^d, \tag{5}$$

where $(\zeta)_+$ equals ζ for positive ζ, zero otherwise. Between two knots this spline is a polynomial of degree d. In our application it is reasonable to model $\hat{g}$ without an intercept, $\beta_0 = 0$, representing the fact that consumption halts when prey are absent. The optimization criterion is

$$F = \mathrm{WSSR} + \alpha \sum_{j=1}^{m} \beta_{j+d}^2, $$

where WSSR represents the weighted sum of squared residuals (3) and α is the smoothing (or penalizing) parameter which determines the complexity of the fitted function. This penalizing factor makes it possible to use a large number of knots (we typically used 20) without the reconstructed function exhibiting spurious features that are not actually supported by the data. The value of α

needs to be determined independently of the other parameters (see below). Plugging equation (5) into equations (4) shows that the right-hand side is a linear function of the parameters $\theta = (\{\beta_i\}_{1 \leq i \leq m+d}, \mu)$, if the values of the 'nonlinear parameters' e, τ and m are taken as given. The fact that the model is conditionally linear in most parameters allows the large number of parameters to be estimated efficiently. It is biologically reasonable to consider $g(z)$ to be a monotonic increasing function of its argument. This assumption leads to a constraint on the parameters of the form $C\theta \geq 0$ for a specific matrix C (see electronic Appendix C for details). The linear optimization problem together with this constraint leads to a standard quadratic programming problem for which standard software solutions exist (see electronic Appendix C). The remaining nonlinear parameters e, τ and m are then estimated (for given α) by the standard simplex method.

The final shape of the fitted functional response is largely determined by the value of the smoothing parameter. We therefore used two different methods to select α as a check on robustness of our estimates, *k-fold cross validation* and *generalized cross validation*. These are standard methods in the smoothing literature, which we briefly describe in electronic Appendix D. In both cases we took pains to avoid overfitting (selecting a too–small value of α, which produces a fitted curve with spurious wiggles and consequently an overestimate of how well the model fits the data). We observed that overfitting is more likely in the more complex models with predator-dependent functional response. This creates a risk of concluding that the predator-dependent model is superior, when in fact it has been misestimated in a way that inflates its goodness of fit. Conservatism in selecting model complexity is therefore essential for our analysis. Trying to simultaneously estimate model complexity and parameter values is a recipe for overfitting (Ellner & Turchin 1995): your numerical optimizer is then searching for the parameter values at which overfitting occurs, and a good optimizer will find them. To select α we therefore fixed the values of the nonlinear parameters e, τ, and m in equations (4) as the averages of their estimates from fitting the parametric models (see table 1), based on all prey-dependent functional responses for $z = \mathcal{N}$, on the ratio-dependent fits for $z = \mathcal{N}/P$ and on all predator-dependent functional responses for $z = \mathcal{N}/P^m$. After α had been selected, we re-estimated e, τ, and m with α fixed. Even fairly substantial changes in the final value of α (up to a factor of ten) have relatively minor effects on the fitted function, in the sense that the choice of e, τ and m when estimating α does not affect which model fits best.

(d) *Comparison of models by bootstrapping*

After fitting the models $g(\mathcal{N})$, $g(\mathcal{N}/P)$ and $g(\mathcal{N}/P^m)$ we use the weighted sum of squared residuals WSSR (1) to compare between the fits. However, two considerations make these 'raw' goodness-of-fit measures unsuitable for direct model selection: first, we do not know if the difference is significant, and second, they were obtained with different α-values. Both problems can be overcome by the use of a parametric bootstrapping procedure, explained here for the example of testing $g(\mathcal{N})$ against $g(\mathcal{N}/P^m)$: the best fit of model $g(\mathcal{N})$ to the data serves as the baseline,

and we create bootstrap data by taking this fitted model and adding to its predicted values a set of bootstrapped residuals (i.e. sampled with replacement from the set of residuals from the baseline). In generating the bootstrapped residuals, the scaling of error variance with $\mathcal{N}$ or P (see §2a) is taken into account by using the scaling relationship to standardize the residuals from the baseline to unit variance, drawing (with replacement) a bootstrap set of residuals, and then reapplying the appropriate error scaling for the value to which the residual is added in the bootstrap data set. Both models, $g(\mathcal{N})$ and $g(\mathcal{N}/P^m)$, are then refitted to these purely prey-dependent bootstrap data. We resampled 1000 bootstrap data sets (which should be sufficiently large for the problem at hand (Efron & Tibshirani 1993)). The distribution of the differences in fit on the bootstrap pseudo-data are then compared by percentiles to the original difference in fit, telling us whether the original difference in fit was larger than expected under the null hypothesis that the data come from the prey-dependent model. In particular, if the original difference in fit is larger than 95% of the differences in fit for the bootstrap data sets, we conclude that the original difference in fit is significant at level 0.05.

5. RESULTS

(a) *Parametric fitting*

In a first test we fitted the parametric functional responses listed in table 1 to the gradients estimated from the artificial data that were used to test the reliability of gradient estimation. To our surprise, even when taking the deterministic data without any noise, the best fitting model was not of the DeAngelis–Beddington type with which the data were created, but the Crowley–Martin type functional response, closely followed by Watt's functional response. This indicates that goodness-of-fit is an insufficient model selection criterion to select between structurally very similar models. However, broad patterns such as the functional response being prey dependent or ratio dependent seem to be identifiable (as found in a more thorough simulation analysis with these two types of model but with different fitting schemes by Jost & Arditi (2000*a*)).

The results of fitting the parametric functional responses to the natural time-series are summarized in table 1. For each class of complexity (Holling type II to Hassell–Varley type I with five fitted parameters and Hassell–Varley type II to Watt with six fitted parameters) the best fits are emphasized. We can see that in the first class the ratio-dependent model always fits best, with reasonable delays that are shorter in the rich-medium experiments 11a and 14c with CC 0.5. Fitting the more complex models gave the same type of delay, although the improvement in fit only amounted to about 5% in data sets 11a and 12a, while it amounted to an impressive 30% in data set 14c. The models without conservation of mass performed reasonably well, but were always beaten by some equally complex (number of parameters) models with conservation of mass. It is interesting to observe that the prey-dependent models fitted best with very small or even zero delays. Indeed, fitting in a first test non-delayed numerical responses made these prey-dependent forms win over their equally complex predator-dependent
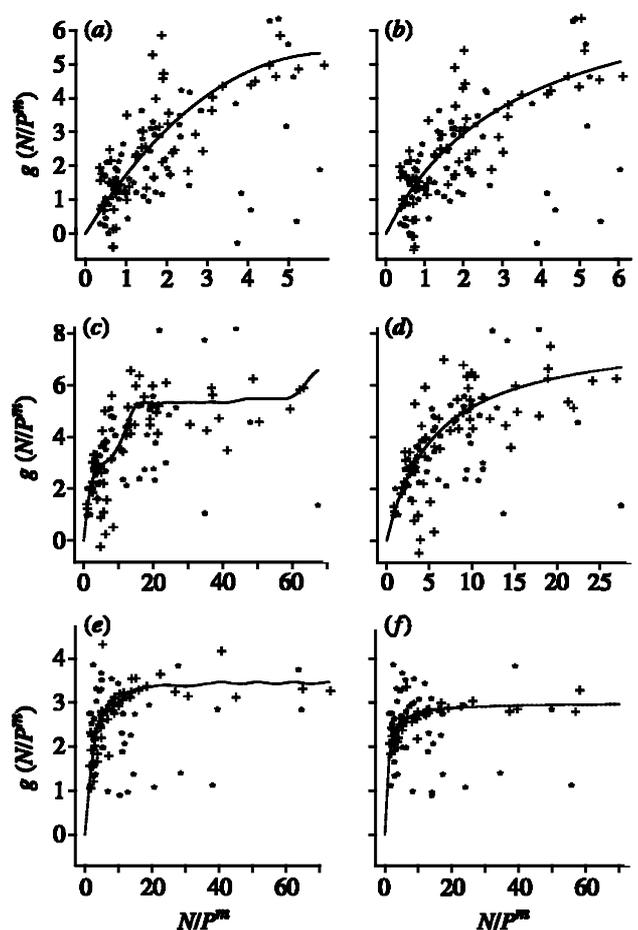

Figure 4. Best fits of the non-parametric generalized Hassell–Varley model $g(\mathcal{N}/P^m)$ (*a*, *c*, *e*) and the parametric Hassell–Varley type II model (*b*, *d*, *f*) for data sets 11a, 12a and 14c (top to bottom). Stars mark the values reconstructed from the prey equation, and plus signs those from the predator equation. Series 11a: (*a*) $g(\mathcal{N}/P^m)$, $m = 0.67$; (*b*) HVII, $m = 0.71$. Series 12a: (*c*) $g(\mathcal{N}/P^m)$, $m = 1.37$; (*d*) HVII, $m = 0.97$. Series 14c: (*e*) $g(\mathcal{N}/P^m)$, $m = 2.41$; (*f*) HVII, $m = 2.58$.

forms. This is consistent with the findings in Jost & Arditi (2000*b*) where non-delayed prey- and ratio-dependent models were fitted to many similar (but shorter) protozoan time-series, and the former fitted better most of the time.

(b) *Non-parametric fitting*

The results of fitting the non-parametric functional responses ($g(\mathcal{N})$, $g(\mathcal{N}/P)$ and $g(\mathcal{N}/P^m)$) are summarized in table 2. The last column for fits of $g(\mathcal{N})$ and $g(\mathcal{N}/P)$ give the bootstrapped significance level of the better fit of the generalized Hassell–Varley type model $g(\mathcal{N}/P^m)$. These show that the latter always fitted significantly better compared to the prey-dependent model, but only in one of the three data sets when compared to the ratio-dependent model (at $p = 0.05$). The remarks in the previous paragraph about the length of the estimated delay apply also to these fits, namely that they are shorter for the richer medium (series 11a and 14c). The conversion efficiencies e vary about a value of 0.5, a level that is higher than the estimates given by Veilleux (1976) of 0.17 for series 11a and 14c, and 0.11 for series 12a (estimating e as the inverse of the fission rates (number of *Paramecium*

Table 2. *Raw results of non-parametric fits of the functional response with estimates and standard deviations*[a] *of e, τ, μ and m, the estimated smoothing parameter α and the significance level of $g(\mathcal{N}/P^m)$ fitting better than $g(\mathcal{N})$ or $g(\mathcal{N}/P)$, respectively* (last column)

(WSSR, weighted sum of squared residuals.)

	α	WSSR	e	τ	μ	significance level
$g(\mathcal{N})$						
11a	10^7	431 ± 65	0.49 ± 0.06	0.00 ± 0.04	1.05 ± 0.12	0.01
12a	10^7	274 ± 52	0.51 ± 0.13	0.30 ± 0.12	1.59 ± 0.31	0.00
14c	111	251 ± 54	0.34 ± 0.11	0.00 ± 0.13	0.88 ± 0.26	0.00
$g(\mathcal{N}/P)$						
11a	3400	403 ± 51	0.44 ± 0.06	0.32 ± 0.06	1.09 ± 0.12	0.07
12a	3.3×10^4	178 ± 30	0.33 ± 0.05	0.82 ± 0.07	1.32 ± 0.14	0.13
14c	100	188 ± 37	0.63 ± 0.23	0.43 ± 0.09	1.88 ± 0.51	0.00
$g(\mathcal{N}/P^m)$						
11a	5800	393 ± 53	0.43 ± 0.06	0.30 ± 0.08	1.06 ± 0.11	0.67 ± 0.14[b]
12a	108	159 ± 25	0.45 ± 0.10	0.81 ± 0.07	1.67 ± 0.26	1.37 ± 0.15[b]
14c	106	133 ± 24	0.68 ± 0.15	0.59 ± 0.06	1.83 ± 0.34	2.41 ± 0.13[b]

[a] Standard deviations were estimated by a parametric bootstrap (1000 bootstrap samples).
[b] *m*-value.

necessary for one *Didinium* fission) in Veilleux (1976, table 3)). The mortality rates are higher for 14c than for 11a (as expected, because 14c has the same laboratory conditions as 11a but with an additional artificial mortality) when fitting $g(\mathcal{N}/P)$ and $g(\mathcal{N}/P^m)$, but not when fitting the prey-dependent model. Figure 4*a,c,e* shows the reconstructed generalized Hassell–Varley functional response for each time-series. Note that each pair of measured prey and predator densities results in two estimates of the functional response (one from the prey equation (4*a*) and the other from the predator equation (4*b*)) indicated in figure 4 by a star or a plus sign, respectively.

6. DISCUSSION

Protozoan predator–prey systems in the laboratory are usually homogeneous (well mixed) and the organisms move around randomly while either hunting or eating. Under these conditions the behavioural context that gives a Holling type II functional response is well approximated; such organisms are thus expected to have a prey-dependent functional response. However, our analysis shows that allowing the functional response to decrease with increasing predator density gives in all three data sets a significantly better fit. This confirms the results from Harrison (1995) who fitted trajectories of the underlying differential equations to Luckinbill's data (same protozoan species as our data) and obtained the best fit with a model that includes predator dependence and a delayed numerical response. Our analysis goes a step further in testing general non-parametric forms of the functional response and in showing the improvement in fit to be significant.

This strong predator dependence seems to be contrary to earlier results (Jost 1998; Jost & Arditi 2000*b*) where we fitted a prey- and a ratio-dependent model to Gause's, Luckinbill's and part of Veilleux's data and always found the prey-dependent model to fit significantly better. However, these earlier results were obtained without a delay in the reproduction equations. Indeed, when we fitted the parametric functional responses in table 1

without a delay, the prey-dependent model also fitted in our analysis better than the ratio-dependent model. This raises the question whether adding a delay improves the fit significantly and is thus justified. We tested this with the bootstrap techniques described in §4 and fitting a non-parametric general Hassell–Varley type functional response with or without a delay in the numerical response, and for all three data sets the improvement in fit was highly significant (at $p = 0.01$). A delayed numerical response seems therefore to be a valid assumption. This delay should usually correspond to the generation time. For protozoans, this would be the time between two fissions. Our estimates of the delay conform quite well to the generation times estimated by Veilleux (1976, table 3*a*), and they are longer for the CC 0.375 treatment than for the CC 0.5 treatment, as would be expected (generation time increases in a poorer environment). The delay seems therefore not only to improve the fit, it also has a sound biological background. Consequently, the predator dependence found when allowing for this delay seems to be genuine.

L. Ginzburg (personal communication) suggested that consumption as well as reproduction should preferably be a function of the average over present and recent population densities rather than an instantaneous rate. In our modelling framework this can be approximated by introducing the same discrete delay in both functional and numerical response in equations (2). We tested this suggestion and found again that the general Hassell–Varley functional response always fitted highly significantly better than the prey-dependent functional response, but only in one of three cases did it fit better than the ratio-dependent model. This additional test shows that our general result is quite robust with respect to the delay structure in the model.

It should be noted here that the parameters r and K (that were estimated from independent experiments and then assumed known in all of the above tests) could easily be estimated in the fitting process because the rate equations are linear in both of them. We tested this possibility, and most of the results mentioned above remain valid;

only the difference between the general Hassell–Varley and the ratio-dependent functional response became smaller or even indetectable (with the estimated m being close to unity).

The mechanisms inducing predator dependence range from direct interference (Beddington 1975) over anti-predator behaviour (Abrams 1984) or aggregation and hunting behaviour (Cosner *et al.* 1999) to spatial hetero-geneity combined with different time-scales (Poggiale *et al.* 1998). In our system, aggregation (due to local prey depletion rather than hunting behaviour; Free *et al.* 1977) seems the most plausible explanation. Veilleux (1976) also detected predator dependence and enumerated two other potential explanations: (i) *Didinium* is, in fact, capable of distinguishing between starved and well-fed prey and selectively attacks the latter, (ii) while there is no direct interference between *Didinium* individuals, they may share a prey; this is observed, especially at high predator concentrations. However, the information is too scant to decide if one of these mechanisms can account for the detected predator dependence. At the level of abstraction on which we worked (modelling a population as a single state variable), predator dependence could also emerge as a combined result of several mechanisms.

While we insisted in §1 on the generality of our approach by taking non-parametric functional responses, it should be tested whether the parametric forms (that are more accessible for theoretical analysis and much simpler to parameterize) already give a sufficiently good description. Figure 4 shows the reconstructed non-parametric Hassell–Varley type functional responses and the fitted parametric Hassell–Varley type II functional responses. The latter seem to perform qualita-tively quite well and have the advantage of having only three parameters. Other parametric forms such as the DeAngelis–Beddington or Crowley–Martin functional responses also performed as well or even better (table 1), so they represent equally valid candidates, but since they are functions of two independent arguments the Hassell–Varley type II form may be advantageous in theoretical work. If there are not sufficient data to estimate the addi-tional parameter m then table 2 suggests that the ratio-dependent type II model (which outperformed in the parametric fits all other functional responses of the same complexity) might also be a good approximation, in any case a better one than the Holling type II model.

The strength of the detected predator dependence ($m = 0.66 - 2.41$) requires some additional comments. Originally m was introduced as a parameter in the interval (0, 1) (Hassel 1978). However, this was due to its use in the discrete model of Nicholson and Bailey; recent estimates in the context of continuous models (Stow *et al.* 1995; Ponsard *et al.* 2000) were often larger than unity. It is presently not clear whether $m > 1$ is biologically reasonable in a differential equation model. Abrams (1997) pointed out that anti-predator behaviour can lead to $m > 1$, but further work is needed in this respect.

In conclusion, the non-parametric approach has allowed us to compare for the *Paramecium–Didinium* interaction two fundamental hypotheses (prey versus predator dependence) rather than specific functional forms. Our results confirm recent findings that even in such a simple protozoan system, predator dependence

occurs and can be quite strong. Allowing for delayed effects was crucial for detecting predator dependence: in previous analyses of the same data with non-delayed predator–prey models, predator dependence appeared to be negligible. For theoretical work which includes predator dependence we suggest that the Hassell–Varley type II form (or even the simpler ratio-dependent type II form) may be an adequate and sufficiently flexible para-metric model.

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