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## From pattern to process: identifying predator–prey models from time-series data

Received: July 13, 2000 / Accepted: September 25, 2001

**Abstract** Fitting nonlinear models to time-series is a technique of increasing importance in population ecology. In this article, we apply it to assess the importance of predator dependence in the predation process by comparing two alternative models of equal complexity (one with and one without predator dependence) to predator–prey time-series. Stochasticities in such data come from both observation error and process error. We consider how these errors must be taken into account in the fitting process, and we develop eight different model selection criteria. Applying these criteria to laboratory data on simple protozoan and arthropod predator–prey systems shows that little predator dependence is present, with one interesting exception. Field data are more ambiguous (either selection depends on the particular criterion or no significant differences can be detected), and we show that both models fit reasonably well. We conclude that, within our modeling framework, predator dependence is in general insignificant in simple systems in homogeneous environments. Relatively complex systems show significant predator dependence more often than simple ones but the data are also often inconclusive. The analysis of such systems should rely on several models to detect predictions that are sensitive to predator dependence and to direct further research if necessary.

**Key words** Functional response · Observation error · Process error · Predator dependence · Model selection · Protozoan dynamics · Arthropod dynamics · Plankton dynamics

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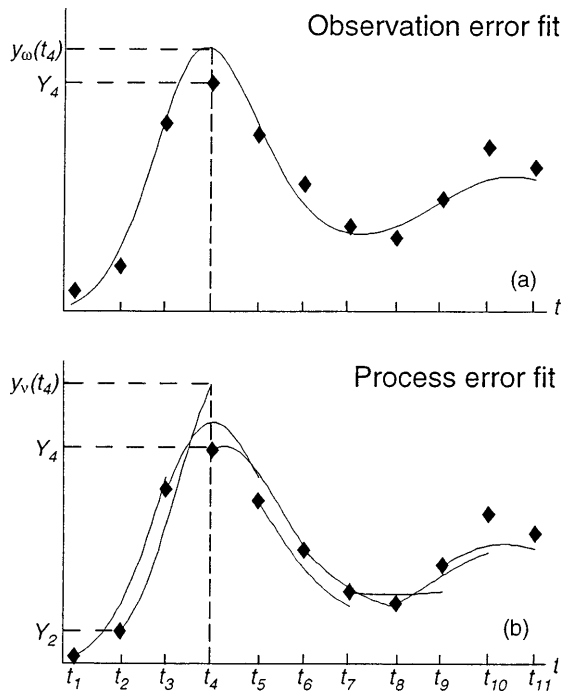
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### Introduction

The relation between predator–prey theory and real population time-series has been the subject of many studies since the early publication of the Lotka–Volterra equations or the Nicholson–Bailey model. The studied systems range from protozoan organisms through arthropod systems and microtine systems to the whole plankton community of lakes (Gause 1935; Huffaker 1958; Turchin and Ellner 2000; Scheffer 1998). Traditionally, model validation is done by comparing the data with the model either qualitatively (stable or cyclic dynamic behavior, length of cycles, amplitudes, etc.) or quantitatively (estimating parameters in the field, and calibrating the model “by hand” to obtain a good fit to the data). Recently, computer power combined with powerful global optimization algorithms has enabled researchers to fit rather complex (mechanistic) nonlinear models to time-series data. One application of these fitting techniques is model selection (Morrison et al. 1987; Carpenter et al. 1994; Harrison 1995; Morris 1997), either to detect a best-fitting model or to show that several models can explain the data. Model selection in predator–prey systems is of particular interest because the functional form of the model can have implications in population management and conservation biology (Yodzis 1994), on stability and persistence of populations (Myerscough et al. 1996), on biological control (Wood and Thomas 1999), or on the spatial distribution of predators (van der Meer and Ens 1997).

In this article, we use model fitting to address the question of detecting predator dependence in the functional response (which links the prey with the predator dynamics, Solomon 1949). Although predator–prey models with a predator-independent functional response (originally termed prey-dependent by Arditi and Ginzburg 1989) rest essentially on top-down mechanisms (Oksanen et al. 1981), predator-dependent models can reflect both bottom-up and top-down relations (DeAngelis et al. 1975; Arditi and Ginzburg 1989; Poggiale et al. 1998; Ponsard et al. 2000). The two views have been tested mostly by comparing equilibrium population abundances along a gradient of enrich-



**Fig. 1.** Fitting a differential equation to a time-series (artificial data for illustrative purposes). **a** All error is assumed to be measurement error and the whole trajectory is fitted at once (*observation-error-fit*, OEF). **b** All error is assumed to be process error and each data point serves as an initial condition to predict the data point  $s$  ( $= 2$  in this graph) steps ahead (*process-error-fit*, PEF)

ment or by reanalyzing data of published functional response experiments (see next section for details). Fitting models to time-series of populations that are not in an equilibrium and applying goodness-of-fit as a criterion approaches the problem from a dynamic point of view.

The method by which models should be fitted to time-series depends on the source of errors in the data (Solow 1995; Hilborn and Mangel 1997). If the underlying process is stochastic and there is no sampling error (no observation error), then predictions are only possible for a limited time into the future, e.g., to the next data point (one-step-ahead fitting). On the other hand, if the underlying process is deterministic and there is observation error only, then the population trajectory (as determined by the model, its parameters, and the initial population size) can be fitted over the whole length of the time-series (see Fig. 1 and Appendix A for notations). We adopted Pascual and Kareiva's (1996) terminology for these two types of fitting, calling the first process-error-fit (PEF) and the second observation-error-fit (OEF).

Most ecological time-series contain both types of error, and methods exist to account for them simultaneously (Reilly and Patino-Leal 1981; Schnute and Richards 1995; Pascual and Kareiva 1996; Bjørnstad et al. 1999). However, these methods are numerically very complicated and time-consuming. Furthermore, they have mostly been used with discrete models; adapting them to continuous models (as used in this article) would further increase the computing time. Thus, the "practical decision usually involves choosing between the two fitting procedures" and "the two assump-

tions are expected to provide two extremes in a range of likely parameter estimates" (quoted from Pascual and Kareiva 1996, who provide an extensive discussion of statistical properties of the two types of fitting).

A PEF approach to detect predator dependence was used by Carpenter et al. (1994) with 7 years of freshwater plankton data in two North American lakes. These authors fitted alternative discrete predator-prey models with predator-independent or predator-dependent functional responses, assuming the parameters to be the same over the whole 7 years. The aim of their paper was mostly methodological, and the actual real data analysis yielded few interpretable results. One problem in their study is that plankton dynamics are more correctly modeled by a continuous system (large populations and overlapping generations) and taking the time between measurements as the prediction time step is an arbitrary choice. Furthermore, parameters might change from one year to the next. A second study (Harrison 1995) used an OEF approach and compared several continuous predator-prey models (differential equations) by fitting them to the protozoan data of Luckinbill (1973). Working with laboratory data, the author assumed stochastic processes to be negligible compared to observation error. A major problem in this study is that Harrison's selection criterion does not take model complexity into account. Unsurprisingly, the model with the largest number of parameters gave the best fit.

We reanalyze here the data of both studies (Carpenter et al. 1994; Harrison 1995), plus other time-series found in the literature, to address the biological problem of detecting whether the importance of predator dependence in the functional response justifies its inclusion in predator-prey models. This analysis will be done by fitting two continuous models (in contrast to the discrete analysis of Carpenter et al. 1994) with a predator-independent and a predator-dependent functional response. Both models have the same number of parameters (avoiding the problems of the Harrison 1995 analysis) and can display the same range of qualitative dynamic behaviors. Goodness-of-fit (based on a least-squares approach) and a measure of prediction error are used as criteria for model selection. In the words of Linhard and Zucchini (1986), we base model selection on measures of discrepancy between the models and the data. The analyzed time-series range from simple protozoan batch cultures through spatially more complex laboratory arthropod systems to complex lake plankton systems (all have the characteristics of a continuous system, i.e., large populations and overlapping generations). Because such data contain both observation and process errors, we apply systematically both a PEF and an OEF (selection of the same model with both types of fits was shown in a simulation analysis to give a more reliable result, Jost and Arditi 2000). This reliability is further extended by using two goodness-of-fit criteria (standard least-squares and a robust criterion) that reflect the uncertainty about the precise distribution of the errors. Bootstrapping is used to obtain a criterion based on the predictive power and to test whether the differences found are significant.

The time-series used are characterized by small size [10–50 data triplets (time, prey, predator)] and by rather large

measurement errors with coefficients of variation (CV) up to 50%. For these reasons, a good fit of a given model does not necessarily mean that it describes the biological processes correctly. This difficulty in model selection based on goodness-of-fit to noisy data has been known since Feller's (1939) early work: he fitted several alternative sigmoid functions successfully to data that were considered at the time to be the "proof" that Verhulst's model for population growth had the character of a physical law. This example illustrates that "multiple process configurations can produce the same pattern" (Cale et al. 1989). Following May's (1989) advice, these serious problems of model fitting can be addressed by "generating pseudo-data for imaginary worlds whose rules are known, and then testing conventional methods for their efficiency in revealing these known rules." We tested the distinguishability of the two models under consideration in a simulation study (Jost and Arditi 2000). Using randomly created predator-prey time-series that have similar characteristics as the data analyzed in this study (in particular, containing both observation and process errors), this study showed that the tested models (see next section) can be identified reliably by goodness-of-fit (with the methods detailed next) from data with such characteristics. Furthermore, the highest reliability can be achieved if both PEF and OEF select the same model.

## Alternative models

Based on the principles of mass conservation (Rosenzweig and MacArthur 1963; Ginzburg 1998) and decomposition of the dynamics of a population into birth and death processes, we write the canonical form of a predator-prey model as

$$\begin{aligned}\frac{dN}{dt} &= f(N)N - g(N, P)P \\ \frac{dP}{dt} &= eg(N, P)P - \mu P\end{aligned}\quad (1)$$

where  $N$  and  $P$  are prey and predator abundances, respectively,  $f$  is the prey growth rate in the absence of a predator,  $\mu$  is the predator mortality rate in the absence of prey, and  $e$  is the conversion efficiency. Predation is represented by the functional response  $g(N, P)$ , which in general depends on both prey and predator abundances.

To fit model 1 to data, we must formulate  $f$  and  $g$  explicitly. For the recruitment function  $f$ , we use a standard logistic growth,  $f(N) = r(1 - N/K)$ , with intrinsic growth rate  $r$  and carrying capacity  $K$ . Many different expressions for the functional response can be found in the literature (see May 1976 and Michalski et al. 1997 for inventories). We choose a standard Holling type II model for the predator-independent (= prey-dependent) case and a ratio-dependent model (Arditi and Ginzburg 1989) for the predator-dependent case:

$$\begin{aligned}\text{Prey dependence, } g(N, P) &= g(N) = \frac{aN}{1+ahN} \\ \text{Ratio dependence, } g(N, P) &= g(N/P) = \frac{aN/P}{1+ahN/P}\end{aligned}\quad (2)$$

where  $a$  is the searching efficiency,  $h$  is the handling time, and  $\alpha$  is an overall searching efficiency for all predators. The dynamics of the prey-dependent model are either stable coexistence, unstable coexistence (limit cycles), or extinction of the predator (Hastings 1997, Chapter 8). In addition to these dynamics, the ratio-dependent model also offers extinction of both prey and predator (Jost et al. 1999; Berezovskaya et al. 2001). These dynamics are also observed in the time-series with which we shall compare the models. The Holling type II model was chosen because it is the most widely used predator-independent functional response. The ratio-dependent model is a predator-dependent functional response that has the same number of parameters and offers, in the given predator-prey context, similar dynamics as the Holling type II model. Alternative predator-dependent models with comparable dynamics (Beddington 1975; DeAngelis et al. 1975; Hassell and Varley 1969) have more parameters.

An alternative to model selection based on discrepancies is hypothesis testing (Linhard and Zucchini 1986). For example, one might use the versatile Hassell-Varley-Holling functional response (Sutherland 1983; Arditi and Akçakaya 1990):

$$g(N, P) = \frac{\alpha NP^{-m}}{1 + ahNP^{-m}}$$

and estimate the additional parameter  $m$  as a quantification of predator dependence. The biological interest in quantifying predator dependence is obvious. We therefore estimate this parameter as well, but we refrain from using it for testing purposes ( $m = 0$  or  $m = 1$ ) because the bootstrapped confidence intervals are not very reliable due to overfitting and algorithmic problems. We also want to concentrate on models that are of interest to practitioners (who rarely can allow for more than two parameters in the functional response).

The controversy around the ratio-dependent model (Ruxton and Gurney 1992; Arditi et al. 1992; Abrams 1994; Akçakaya et al. 1995; Abrams and Ginzburg 2000) requires some additional comments. Ratio-dependent predation was originally proposed as a simple phenomenological model that accounts for general empirical patterns in food chains (Arditi and Ginzburg 1989; Arditi et al. 1991). Most criticisms against ratio dependence revolved around this phenomenological character. Mechanisms leading to ratio dependence have since then been demonstrated (Poggiale et al. 1998; Cosner et al. 1999; Arditi et al. 2001). However, it should be noted that, in highly complex systems such as lakes, there can be too many important processes at work to incorporate them all in a mechanistically derived model (spatial aggregation, defense mechanisms, refuges, etc.). In such situations, we still consider phenomenological models to be a reasonable option. Predator dependence is a common occurrence in natural populations (Arditi and Akçakaya 1990; see review in Sutherland 1996), and it can explain the observed positive correlations between consecutive trophic level abundances along a gradient of productivity (Arditi et al. 1991; Mazumder 1994; McCarthy et al. 1995; Mazumder and Havens 1998; Ponsard et al. 2000).

Ratio dependence is just one possible way to include predator dependence, but it does so in a parsimonious way and allows for direct comparison with a prey-dependent response. A better fit of the ratio-dependent model over the prey-dependent model (or vice versa) cannot and will not be interpreted as a proof that this model is correct but only that it better approximates the actual occurrence of predator dependence.

## Materials and methods

### Time-series

Two kinds of time-series data are analyzed: data retrieved from the published literature and unpublished original data of phyto- and zooplankton dynamics in Lake Geneva. Only data with strong dynamics (sustained or damped oscillations) and allowing reasonable fits with both PEF and OEF are considered. Because the difference between the two functional responses that we compare is in the influence of predator abundance, we request that predator abundance varies by at least a factor of two over time. Most of these data were obtained by scanning the graphics in the publications and extracting the data with the software DATATHIEF (Macintosh). This process unavoidably introduces some error, but this error was of minor importance compared to the final residuals in the fits. The data were usually published with no indication of the observation error, or it was measured once and assumed to be stationary (Carpenter et al. 1994; Huffaker 1958) (see Table 1 for a listing of all data that are analyzed).

The data can be assigned to three categories: (1) protozoa and plankton grown in the laboratory in batch cultures, (2) mites grown in the laboratory, and (3) plankton measured directly in freshwater lakes. The batch cultures were usually grown in small flasks and the medium was renewed

periodically when counting the individuals. Gause (1935) used destructive counting, but because this was done on a small proportion of the culture (1.7%), we have chosen to neglect this additional mortality. Luckinbill (1973) and Veilleux (1979) both used nondestructive counting. One additional data set of Luckinbill was obtained directly from the author. The marine plankton data of Flynn and Davidson (1993) are those of static batch cultures without aeration, stirred every day before sampling. The data sets flynn1b, flynn2b, and flynn2c were shortened from their Figs. 1b, 2b, and 2c, respectively, because there was an obvious change in parameters during the experiment, detectable by an abrupt change in dynamics and described by the authors as the onset of strong cannibalism among predators. The data sets consist of the data before the change. The mites of Gause et al. (1936) were held in open glass tubes, while Huffaker used more complex setups with prey patches arranged in two (Huffaker 1958) or three (Huffaker et al. 1963) dimensions. The data for Paul Lake and Tuesday Lake (Carpenter et al. 1993) were given directly in tabulated form within the publication, and some missing data points were obtained from the authors. Carpenter et al. (1994) fitted their models to the whole time-series from 1984 to 1990, whereas we treated each year individually to allow for year-to-year differences in physical conditions.

The data from Lake Geneva (Switzerland and France) were collected as part of the lake monitoring program of the International Commission for Protection of Lake Geneva Against Pollution (CIPEL) and cover the years 1986 to 1993. The sampling methods are described in annual reports (e.g., CIPEL 1995). A short description can also be found in Gawler et al. (1988). Phytoplankton were sampled with a Pelletier bell-shaped integrating sampler from 0 to 10m water depth. Zooplankton were sampled by vertical tows from a depth of 50m with coupled nets. Plankton biomass was calculated from abundance and estimated biovolume. Phytoplankton 50 $\mu$ m or less (in length) and biovolume of

**Table 1.** The data sets

Name of data set	Source	Prey	Predator	Type of data
Protozoa and plankton (batch culture)				
gause 1	1	<i>Schizosaccharomyces pombe</i>	<i>Paramecium bursaria</i>	Number of individuals
gause 3, -4	1	<i>Saccharomyces exiguus</i>	<i>Paramecium aurelia</i>	Number of individuals
luckin 1a, -1b, -3a, -4a, -4b, -5	2	<i>Paramecium aurelia</i>	<i>Didinium nasutum</i>	Number of individuals
veill 8, -10	3	<i>Paramecium aurelia</i>	<i>Didinium nasutum</i>	Number of individuals
wilh 4.2, -4.4, -5.27, -5.28, -5.29, -5.30	4	<i>Escherichia coli</i>	<i>Tetrahymena thermophila</i>	Biovolume
flynn 1b, -1c, -2b, -2c	5	<i>Isochrysis galbana</i>	<i>Oxyrrhis marina</i>	Number of cells
Mites (laboratory)				
gauset 2a, -c, -d, -e, -f	6	<i>Aleuroglyphus agilis</i>	<i>Cheyletus eruditus</i>	Number of individuals
huff 11, -12, . . . , -18	7	<i>Eotetranychus sexmaculatus</i>	<i>Typhlodromus occidentalis</i>	Number of individuals
huff 63-3, -63-4	8	<i>Eotetranychus sexmaculatus</i>	<i>Typhlodromus occidentalis</i>	Number of individuals
Plankton (lakes)				
paul 84, -85, . . . , -90, tues 84, -85, . . . , -90	9	Edible phytoplankton	Zooplankton	Biomass
edPhy 86, -87, . . . , -93	10	Edible phytoplankton	Herbivorous zooplankton	Biomass
totPhy 86, -87, . . . , -93	10	Total phytoplankton	Herbivorous zooplankton	Biomass

Sources are (1) Gause (1935); (2) Luckinbill (1973); (3) Veilleux (1979); (4) Wilhelm (1993); (5) Flynn and Davidson (1993); (6) Gause et al. (1936), table 2; (7) Huffaker (1958); (8) Huffaker et al. (1963); (9) Carpenter et al. (1993b); (10) CIPEL reports (1986-1993)

Numbers or letters separated by a comma refer to further data sets with the same basic name; e.g., gause 1, -3 refer to data sets gause 1 and gause 3; usually, these numbers refer to the figures or tables within the cited publication, except for plankton data where they refer to the year in which the data were collected

$10^4 \mu\text{m}^3$  or less were considered edible phytoplankton. Herbivorous zooplankton were identified by species and age class: cladocerans (mainly *Daphnia* and *Bosmina*), calanoids (*Eudiaptomus*), and cyclopoids for the age classes nauplii to copepodites stage 3 (higher age classes were considered carnivorous). The samples were taken at station SHL2, at the center of the lake, midway between Evian (France) and Lausanne (Switzerland) (lake depth, 309 m). Plankton were usually sampled twice a month. The observation error was not measured, but the collecting scientists estimate the coefficient of variation (CV) to be in the range of 10%–20% for an individual sample, as in Carpenter et al. (1994). However, there are important heterogeneities in the lake, and the CV between several samples in the same area at the same time can be much larger (Pinel-Alloul et al. 1999). For this reason, we used in the fitting a prudent CV of 50%, which is considered realistic for zooplankton but somewhat pessimistic for phytoplankton. As in the case of Carpenter's data (see above), we fit our models to each annual series independently, starting with the onset of plankton growth in the spring and ending with the plankton decline in the autumn.

#### Error functions for regression and model selection

As explained in the Introduction, we considered two types of errors separately, i.e., measurement error  $\omega$  (imprecise sampling) and dynamic noise  $\nu$  (due to environmental stochasticities, demographic stochasticity, and differences between the real biological process and its mathematical description). The prediction horizon with PEF is traditionally one time step ahead (Carpenter et al. 1994; Dennis et al. 1995). However, this time horizon might be too short to detect nonlinear relations or simply to observe sufficiently strong dynamics compared to the noise in the data. For these reasons, Ellner and Turchin (1995) predicted the dynamics  $s$  time steps ahead, with  $s$  chosen in such way that the autocorrelation with the predictor drops below 0.5. We followed this example, but the optimal choice of  $s$  is currently under debate, and we refer the reader to Ellner and Turchin (1995) for a broader discussion.

Goodness-of-fit is estimated with a least-squares method. The details are found in Appendix A, and we only mention here the general assumptions and the resulting goodness-of-fit measures. We assume that the (observation or process) error in the densities is of a multiplicative type that is stationary on log scale. This type is typical for population data in general (Dennis et al. 1995; Hilborn and Mangel 1997). It was used and justified for plankton in particular by Carpenter et al. (1994). For protozoan and arthropod data, this choice also seems reasonable (Wilhelm 1993; Huffaker 1958). This estimation makes the OEF equivalent to standard least-squares on a log scale (criterion  $\chi_\omega^2$  in Appendix A) and the PEF equivalent to conditional least-squares (Dennis et al. 1995) on a log scale (criterion  $\chi_\nu^2$  in Appendix A).

Although stationarity (on log scale) of observation error or process error is generally accepted, there can be con-

siderable doubt about the normality of the log-transformed values. Regressions with the sum of squares criteria  $\chi_\kappa^2$  ( $\kappa = \omega, \nu$ ) are very sensitive to outliers (data points that are farther away from their real value than would be expected with a normal distribution) with respect to parameter estimation and model selection (Linhard and Zucchini 1986). We therefore used as a second error type the Laplacian (or double exponential) distribution on a log scale, resulting in the goodness-of-fit criteria  $\chi_\kappa^L$ ,  $\kappa = \omega, \nu$  ("least absolute deviations"; see Appendix A). The details of the numerical minimization procedures used to compute  $\chi_\kappa^2$  and  $\chi_\kappa^L$  can be found in Appendix B.

In a further analysis, we estimated the expectation  $E(\chi_\kappa^2)$  and the improved estimate of prediction error  $IE$  (as described in Efron and Tibshirani 1993) by residual bootstrapping to compare the predictive power of the two models. See Appendix B for a detailed technical description of this method.

#### Model selection

Before performing model selection, we have to test whether the fitted model describes the data reasonably well. The statistic

$$\ell = \Gamma\left(\frac{\ell^2}{2}, \frac{DF}{2}\right), \quad (3)$$

where  $DF$  is the degrees of freedom (number of predicted data points minus number of parameters) and  $\Gamma$  is the incomplete gamma function, is a measure of the probability of exceeding the quantity  $\chi^2$  by chance (Press et al. 1992). The higher this value, the better the goodness-of-fit. However, Eq. 3 is strictly correct only for models that are linear in the parameters (Press et al. 1992). We must rely on the values of Eq. 3 computed in our previous simulation analysis (Jost and Arditi 2000) (where they ranged from 0.01 to 0.9) to know which goodness-of-fit levels can be expected with our nonlinear models. Assuming a larger discrepancy between the theoretical model and the real process, we accept all fits with a value of  $\ell$  above 0.001. If  $\ell$  is smaller than 0.001, the fit is considered nonacceptable. Note that the use of Eq. 3 in a least-squares framework does not permit estimating the variance–covariance matrix (used to compute  $\chi^2$ ) independently (Press et al. 1992). We therefore set the standard deviation to the highest value that was reported for our data (see Appendix A for details).

We could not find a function similar to Eq. 3 in the case of Laplacian error  $\chi^L$ . These fits were thus accepted if the  $\chi^2$  fit was accepted. Finally, the  $IE$  criterion was accepted if  $E(\chi^2)$  gave  $\ell$  values above 0.001.

Model selection is now based on the goodness-of-fit criteria  $\chi^2$ ,  $\chi^L$ , and on the prediction error criterion  $IE$ . We require  $\chi^2$  or  $\chi^L$  to differ by at least 5% between the two models to be considered significantly different. [In the simulation analysis (Jost and Arditi 2000), this requirement reduced the proportion of wrong identifications below 5%.] The  $IE$  for the two models is compared directly with a standard  $t$  test ( $\alpha = 0.05$ ). The discussion is based solely on

**Table 2.** Results of fits to time-series data

Data characteristics			Process-error-fit					Observation-error-fit				
Name	$n$	dyn.	$s$	$\chi_v^2$	$\chi_v^L$	$IE_v$	$\bar{m} \pm \sigma_m$	$\chi_\omega^2$	$\chi_\omega^L$	$IE_\omega$	$\bar{m} \pm \sigma_m$	
gause 1	18	<i>st</i>	2	r <i>st</i>	p <i>st</i>	p <sup>†</sup>	0.13 ± 0.07	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.18 ± 0.05	
gause 3	18	<i>l</i>	2	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.01 ± 0.03	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.00*	
gause 4	19	<i>l</i>	2	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.31 ± 0.10	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.17 ± 0.09	
luckin 1a	35	<i>l</i>	3	p <i>st</i>	p <i>st</i>	p	0.06 ± 0.04	p <i>l</i>	p <i>l</i>	p <sup>†</sup>	0.00*	
luckin 1b	24	<i>l</i>	3	p <i>st</i>	p <i>st</i>	p <sup>†</sup>	0.12 ± 0.11	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.00*	
luckin 3	16	<i>l</i>	3	r <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.65 ± 0.18	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.01 ± 0.01	
luckin 4a	27	<i>l</i>	3	p <i>st</i>	p <i>st</i>	p <sup>†</sup>	0.10 ± 0.06	p <i>l</i>	p <i>l</i>	p <sup>†</sup>	0.00*	
luckin 4b	21	<i>l</i>	3	p <i>l</i>	p <i>l</i>	p <sup>†</sup>	0.00*	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.01 ± 0.01	
luckin 5	62	<i>l</i>	3	p <i>st</i>	p <i>st</i>	p	0.01 ± 0.01	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.00*	
veill 8	87	<i>l</i>	3	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.21 ± 0.05	r <sup>†</sup> <i>l</i>	r <sup>†</sup> <i>l</i>	r <sup>†</sup>	1.03 ± 0.01	
veill 10	20	<i>l</i>	3	p <i>l</i>	p <i>st</i>	p <sup>†</sup>	0.23 ± 0.05	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.22 ± 0.06	
flynn 1b	14	<i>t</i>	4	r <sup>†</sup> <i>t</i>	r <sup>†</sup> <i>t</i>	r <sup>†</sup>	0.52 ± 0.04	r <sup>†</sup> <i>t</i>	r <sup>†</sup> <i>t</i>	r <sup>†</sup>	0.38 ± 0.02	
flynn 1c	21	<i>st, e</i>	4	r <sup>†</sup> <i>e</i>	r <sup>†</sup> <i>e</i>	r <sup>†</sup>	0.39 ± 0.02	r <sup>†</sup> <i>e</i>	r <sup>†</sup> <i>e</i>	r <sup>†</sup>	1.98 ± 0.19	
flynn 2b	28	<i>st, e</i>	4	r <sup>†</sup> <i>e</i>	r <sup>†</sup> <i>e</i>	r <sup>†</sup>	0.58 ± 0.06	r <sup>†</sup> <i>e</i>	r <sup>†</sup> <i>e</i>	r <sup>†</sup>	0.54 ± 0.08	
flynn 2c	28	<i>st, e</i>	4	r <sup>†</sup> <i>e</i>	r <sup>†</sup> <i>e</i>	r <sup>†</sup>	0.51 ± 0.13	r <sup>†</sup> <i>e</i>	r <sup>†</sup> <i>e</i>	r <sup>†</sup>	0.53 ± 0.16	
wilh 4.2	16	<i>st, e</i>	4	r <i>st</i>	r <i>e</i>	p	1.00 ± 0.01	p <i>st</i>	p <i>ss</i>	p <sup>†</sup>	0.00*	
wilh 4.4	17	<i>st, e</i>	3	r <sup>†</sup> <i>ss</i>	r <sup>†</sup> <i>ss</i>	r <sup>†</sup>	1.00 ± 0.01	r <sup>†</sup> <i>st</i>	r <sup>†</sup> <i>st</i>	r <sup>†</sup>	0.99 ± 0.04	
wilh 5.27	17	<i>e</i>	4	p <i>st</i>	r <sup>†</sup> <i>ss</i>	p	0.00*	p <i>st</i>	r <i>e</i>	p	0.13 ± 0.16	
wilh 5.28	22	<i>st, e</i>	5	r <sup>†</sup> <i>e</i>	r <sup>†</sup> <i>e</i>	r <sup>†</sup>	1.10 ± 0.04	p <sup>†</sup> <i>pe</i>	r <sup>†</sup> <i>t</i>	p <sup>†</sup>	0.08 ± 0.08	
wilh 5.29	19	<i>st</i>	3	p <sup>†</sup> <i>ss</i>	r <sup>†</sup> <i>ss</i>	p <sup>†</sup>	0.43 ± 0.04	r <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>ss</i>	p <sup>†</sup>	0.99 ± 0.05	
wilh 5.30	18	<i>st, e</i>	4	p <sup>†</sup> <i>pe</i>	r <sup>†</sup> <i>ss</i>	p <sup>†</sup>	0.40 ± 0.14	p <sup>†</sup> <i>t</i>	p <sup>†</sup> <i>t</i>	p <sup>†</sup>	0.31 ± 0.05	
gauset 2a	10	<i>e</i>	1	p <i>l</i>	p <i>l</i>	p	0.00 ± 0.02	p <i>l</i>	p <i>l</i>	p <sup>†</sup>	0.18 ± 0.16	
gauset 2c	10	<i>e</i>	1	p <i>l</i>	p <i>st</i>	r	0.26 ± 0.52	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.00*	
gauset 2d	10	<i>e</i>	1	p <i>l</i>	p <i>l</i>	p	0.00*	p <i>l</i>	p <i>l</i>	p	0.29 ± 0.14	
gauset 2e	9	<i>e</i>	1	p <i>l</i>	p <i>l</i>	r	0.05 ± 0.12	p <i>l</i>	p <i>l</i>	p	0.00*	
gauset 2f	9	<i>e</i>	1	r <i>e</i>	r <i>st, e</i>	r <sup>†</sup>	0.76 ± 0.21	r <sup>†</sup> <i>e</i>	r <sup>†</sup> <i>e</i>	r <sup>†</sup>	0.83 ± 0.23	
huff 11	12	<i>e, l</i>	3	r <i>st</i>	r <i>st</i>	p	1.00 ± 0.22	r <i>st</i>	r <i>st</i>	r	0.80 ± 0.07	
huff 12	13	<i>e</i>	3	p <i>l</i>	r <i>e</i>	p	0.02 ± 0.05	p <i>l</i>	p <i>l</i>	p	0.53 ± 0.16	
huff 13	10	<i>e</i>	2	p <i>l</i>	p <i>l</i>	p	0.47 ± 0.18	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.28 ± 0.15	
huff 14	10	<i>e</i>	2	p <i>l</i>	p <i>l</i>	p <sup>†</sup>	0.33 ± 0.12	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.33 ± 0.11	
huff 15	11	<i>e, l</i>	3	r <i>st</i>	p <i>l</i>	p	0.57 ± 0.08	r <i>st</i>	p <i>l</i>	r	0.47 ± 0.06	
huff 16	11	<i>e, l</i>	3	p <i>l</i>	p <i>l</i>	p	0.63 ± 0.19	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.38 ± 0.09	
huff 17	12	<i>e</i>	3	r <i>st, e</i>	r <i>st</i>	p	0.95 ± 0.04	p <i>l</i>	p <i>l</i>	p	0.55 ± 0.18	
huff 18	35	<i>l</i>	4	r <i>st</i>	r <i>st</i>	r	0.91 ± 0.07	p <i>l</i>	p <i>l</i>	p	0.00*	
huff 63-3	58	<i>l</i>	4	p <i>st</i>	p <i>st</i>	p	0.23 ± 0.04	p <i>st</i>	p <i>st</i>	p	0.10 ± 0.04	
huff 63-4	23	<i>l</i>	3	p <i>l</i>	r <i>st</i>	p	0.19 ± 0.08	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>l</i>	p <sup>†</sup>	0.00*	
paul 84	13	( <i>st</i> )	2	r <sup>†</sup> <i>ss</i>	r <sup>†</sup> <i>ss</i>	r <sup>†</sup>	6.45 ± 3.17	p <sup>†</sup> <i>st</i>	r <sup>†</sup> <i>t</i>	p <sup>†</sup>	0.38 ± 0.51	
paul 85	17	<i>st</i>	2	p <i>st</i>	p <i>ss</i>	p	0.09 ± 0.04	p <i>ss</i>	p <i>st</i>	p	0.01 ± 0.02	
paul 86	14	( <i>st</i> )	2	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.28 ± 0.34	p <sup>†</sup> <i>st</i>	r <sup>†</sup> <i>t</i>	r <sup>†</sup>	0.46 ± 0.30	
paul 87	15	( <i>st</i> )	2	p <i>st</i>	p <i>st</i>	p	0.49 ± 0.60	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.02 ± 0.05	
paul 88	15	( <i>l</i> )	2	r <sup>†</sup> <i>ss</i>	r <sup>†</sup> <i>ss</i>	r <sup>†</sup>	0.31 ± 0.42	r <sup>†</sup> <i>t</i>	p <sup>†</sup> <i>st</i>	r <sup>†</sup>	1.37 ± 0.11	
paul 89	13	<i>l</i>	2	p <i>ss</i>	r <i>st</i>	p	0.04 ± 0.02	= <i>st</i>	p <sup>†</sup> <i>l</i>	=	0.01 ± 0.03	
paul 90	16	( <i>l</i> )	2	p <i>st</i>	r <i>ss</i>	r	0.13 ± 0.22	r <i>st</i>	r <i>st</i>	r	1.01 ± 0.31	
tues 84	11	<i>st</i>	2	p <i>ss</i>	r <i>ss</i>	r <sup>†</sup>	0.12 ± 0.14	p <sup>†</sup> <i>st</i>	r <sup>†</sup> <i>t</i>	p <sup>†</sup>	0.00*	
tues 85	13	<i>st</i>	2	r <i>e</i>	r <i>e</i>	p	0.41 ± 1.57	p <i>l</i>	p <i>t</i>	p <sup>†</sup>	0.00*	
tues 86	14	( <i>l</i> )	2	r <sup>†</sup> <i>st</i>	r <sup>†</sup> <i>st</i>	p <sup>†</sup>	1.32 ± 2.10	p <sup>†</sup> <i>l</i>	r <sup>†</sup> <i>t</i>	p <sup>†</sup>	0.19 ± 0.14	
tues 87	15	( <i>l</i> )	2	p <i>st</i>	p <i>pe</i>	p	0.00*	p <sup>†</sup> <i>l</i>	r <sup>†</sup> <i>t</i>	p <sup>†</sup>	0.01 ± 0.01	
tues 88	13	( <i>l</i> )	2	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.00*	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.00*	
tues 89	11	<i>st</i>	2	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.00*	p <sup>†</sup> <i>st</i>	r <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.00*	
tues 90	19	( <i>st</i> )	2	p <i>ss</i>	r <i>ss</i>	r <sup>†</sup>	0.89 ± 0.33	p <sup>†</sup> <i>l</i>	p <sup>†</sup> <i>t</i>	p <sup>†</sup>	0.01 ± 0.04	
edPhy 86	14	( <i>l</i> )	2	r <i>ss</i>	p <i>ss</i>	p	1.59 ± 0.27	p <i>st</i>	r <i>ss</i>	p	0.08 ± 0.07	
edPhy 87	13	( <i>st</i> )	2	p <i>st</i>	p <i>st</i>	p <sup>†</sup>	0.00*	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.00*	
edPhy 88	13	( <i>st</i> )	2	p <i>st</i>	p <i>l</i>	p <sup>†</sup>	0.00*	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>t</i>	p <sup>†</sup>	0.00*	
edPhy 89	13	( <i>l</i> )	2	p <i>ss</i>	r <i>st</i>	r <sup>†</sup>	0.00*	r <sup>†</sup> <i>st</i>	r <sup>†</sup> <i>t</i>	r <sup>†</sup>	1.08 ± 0.03	
edPhy 90	14	( <i>st</i> )	2	r <sup>†</sup> <i>ss</i>	r <sup>†</sup> <i>ss</i>	r <sup>†</sup>	1.05 ± 0.03	r <sup>†</sup> <i>st</i>	r <sup>†</sup> <i>st</i>	r <sup>†</sup>	1.02 ± 0.05	
edPhy 91	12	( <i>st</i> )	2	r <i>ss</i>	p <i>ss</i>	r <sup>†</sup>	0.97 ± 0.07	r <sup>†</sup> <i>st</i>	r <sup>†</sup> <i>st</i>	r <sup>†</sup>	1.02 ± 0.01	
edPhy 92	11	<i>st</i>	2	p <i>ss</i>	p <i>ss</i>	r	0.14 ± 0.15	r <i>st</i>	r <i>st</i>	p <sup>†</sup>	1.04 ± 0.01	
edPhy 93	12	<i>st</i>	3	r <i>st, e</i>	r <i>e</i>	r <sup>†</sup>	1.00 ± 0.01	r <sup>†</sup> <i>t</i>	r <sup>†</sup> <i>t</i>	r <sup>†</sup>	1.00 ± 0.01	
totPhy 86	14	( <i>st</i> )	3	p <i>t</i>	r <i>ss</i>	r	0.95 ± 0.23	r <i>t</i>	r <i>t</i>	r	1.29 ± 0.04	
totPhy 87	13	( <i>st</i> )	2	p <i>ss</i>	p <i>ss</i>	p <sup>†</sup>	0.00*	p <i>st</i>	p <i>t</i>	r <sup>†</sup>	0.00*	
totPhy 88	15	( <i>l</i> )	2	p <i>ss</i>	r <i>ss</i>	r	0.00*	p <i>st</i>	p <i>st</i>	p	0.17 ± 0.10	
totPhy 89	14	( <i>l</i> )	2	p <i>st</i>	r <i>ss</i>	r <sup>†</sup>	0.00*	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.00*	

**Table 2.** Continued

Data characteristics			Process-error-fit					Observation-error-fit				
Name	<i>n</i>	dyn.	<i>s</i>	$\chi_v^2$	$\chi_v^L$	$IE_v$	$\bar{m} \pm \sigma_m$	$\chi_\omega^2$	$\chi_\omega^L$	$IE_\omega$	$\bar{m} \pm \sigma_m$	
totPhy 90	14	<i>st</i>	2	p <sup>†</sup> <i>st</i>	r* <i>ss</i>	p <sup>†</sup>	0.08 ± 0.09	p <sup>†</sup> <i>st</i>	p <sup>†</sup> <i>st</i>	p <sup>†</sup>	0.00*	
totPhy 91	16	( <i>l</i> )	2	p <i>ss</i>	p <i>ss</i>	r*	0.13 ± 0.11	p <sup>†</sup> <i>st</i>	r* <i>st</i>	p <sup>†</sup>	0.00*	
totPhy 92	16	( <i>l</i> )	2	r <sup>†</sup> <i>ss</i>	r* <i>ss</i>	r <sup>†</sup>	1.03 ± 0.02	p* <i>t</i>	p* <i>l</i>	p <sup>†</sup>	0.00*	
totPhy 93	16	( <i>l</i> )	2	r <sup>†</sup> <i>ss</i>	r <sup>†</sup> <i>ss</i>	r	0.99 ± 0.05	p <sup>†</sup> <i>l</i>	p* <i>l</i>	p*	0.00*	

The data sets are described by their length *n* and their apparent dynamic behavior (dyn.) (in parentheses if difficult to decide): *st* for stable nontrivial equilibrium, *ss* for strongly stable equilibrium, *l* for limit cycle, *e* for extinction of both populations, *pe* for extinction of the predator only, and *t* for transient trajectory. For each type of fit (PEF or OEF), the better-fitting model is indicated (p for prey-dependent and r for ratio-dependent) with criteria  $\chi_k^2$ ,  $\chi_k^L$  (together with the dynamic behaviour of the selected model with the estimated parameters) and improved estimate of prediction error (*IE*)

The bootstrap estimate of the predator dependence parameter *m* is given as  $\alpha$ -trimmed mean estimate ± standard deviation ( $\alpha = 0.05$ ); *s* is the prediction horizon in PEF

Significance of model selection is indicated by a <sup>†</sup> ( $\ell > 0.001$  with CV = 0.5) or by a <sup>‡</sup> ( $\ell > 0.001$  with CV = 0.1); \* indicates ambiguity due to a low difference between the fits to each model; the absence of a superscript indicates a nonacceptable fit (see text for definitions of significance and acceptability)

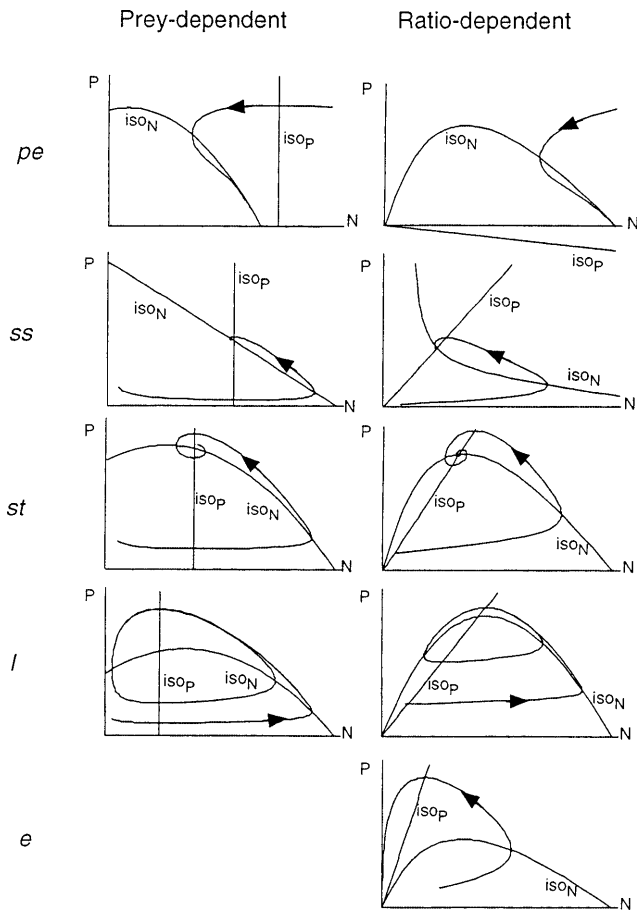
\* Indicates that both  $\bar{m}$  and  $\sigma_m$  are smaller than 0.005

the acceptable fits that are significant (indicated in Table 2 by <sup>†</sup> or <sup>‡</sup>).

A qualitative comparison between the dynamic pattern of the data and the behavior of the (winning) fitted model is used as a second criterion for the adequacy of the model. These qualitative dynamics are classified as strongly stable equilibrium (*ss*) when the trajectory converges to the equilibrium after one oscillation at most, stable equilibrium (*st*) if there is more than one oscillation before stabilization, limit cycle (*l*), extinction of the predator only (*pe*), extinction of both populations (*e*), or transient if no equilibrium state is reached (*t*). See Fig. 2 for an illustration of the different types.

## Results

The detailed fitting results (model selection per type of fitting and per criterion) with additional information on each time-series (size and apparent dynamics, estimates of *m*) are reported in Table 2. To facilitate their interpretation, the essential model selection results are condensed in Table 3 applying the following rules: for each time-series, a “winning” model is selected if all acceptable significant fits (among both types of fitting and with the three different criteria) identify the same model. Otherwise, the time-series is marked as ambiguous. For the lake data, the same procedure was also applied separately for both types of fitting. Furthermore, we indicate if the qualitative dynamics (Fig. 2) of the selected fits correspond to the apparent dynamics of the time-series. Because extinction is not possible in the prey-dependent model, we assume correct detection of the qualitative behavior if the fit shows limit cycle behavior (the closest to extinction that this model can produce). Figure 3 shows two example fits in time space for OEF and PEF; Fig. 4 presents all significant fits in phase space (for easier comparison with Fig. 2) to give an idea of the data and the fitted trajectories in the case of OEF.



**Fig. 2.** The different dynamic behaviors that are distinguished in the data and in the fitted models. Each graph shows the phase space with isoclines of prey (*iso<sub>N</sub>*) and predator (*iso<sub>P</sub>*) and an example trajectory. *pe*, extinction of the predator only; *ss*, strongly stable systems; *st*, stable systems; *l*, limit cycles; *e*, extinction of both populations (only possible in the ratio-dependent model)

**Table 3.** Summary of model selections

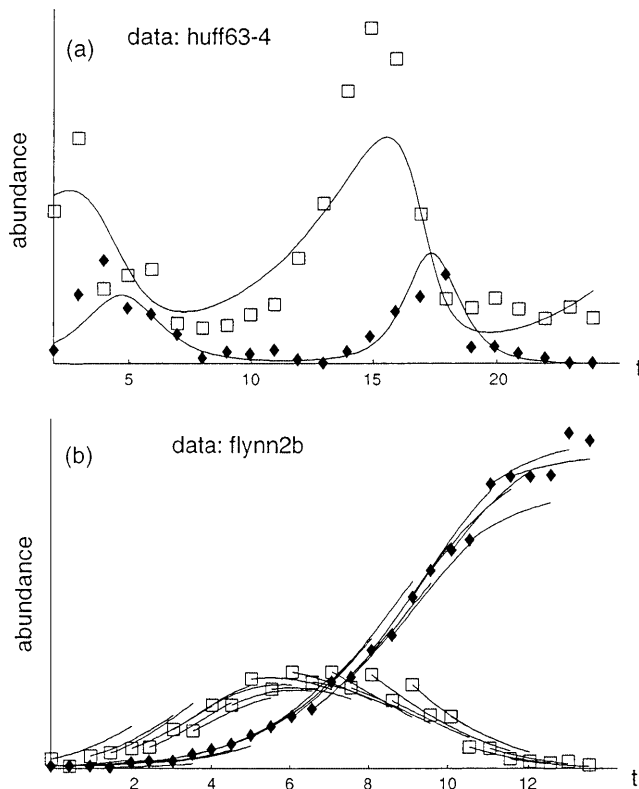
Data	Prey-dependent	Ratio-dependent	Ambiguous
Gause (protozoa)	3 (1)	0	0
Luckinbill, Veilleux	6 (6)	0	2
Flynn and Davidson	0	4 (4)	0
Wilhelm	3 (1)	1 (1)	2
Gause (mites)	2 (2)	1 (1)	2
Huffaker	4 (4)	0	6
Paul Lake	2 (2)	1 (0)	4
Tuesday Lake	4 (2)	0	3
Lake Geneva (edible)	2 (1)	4 (2)	2
Lake Geneva (total)	4 (1)	0	4

	PEF	OEF	PEF	OEF	PEF	OEF
Paul Lake	1 (1)	2 (2)	0	2 (0)	6	3
Tuesday Lake	2 (1)	6 (3)	1 (0)	0	4	1
Lake Geneva (edible)	2 (1)	2 (2)	1 (1)	4 (3)	5	2
Lake Geneva (total)	2 (1)	5 (3)	2 (1)	0	4	3

The first part of the table lists for each group of time-series the number of times that each model was selected by both fitting types, with the number of correct qualitative dynamics in parentheses; the remaining number of ambiguous (or unacceptable) model selections are listed in the last column

The second part of the table treats process-error-fit (PEF) and observation-error-fit (OEF) separately for lakes



**Fig. 3.** Two examples illustrating (a) OEF of a prey-dependent model to Huffaker's data (time measured in weeks) and (b) PEF ( $s = 4$ ) of a ratio-dependent model to Flynn and Davidson's data (time measured in days)

## Protozoan and plankton data in batch cultures

As shown in Table 2, the protozoan and plankton data give the most significant results. With Gause's three data sets, the prey-dependent model wins every time. This lack of predator dependence is confirmed by Luckinbill's and Veilleux's data (both with similar organisms), in which six prey-dependent time-series are identified and two are ambiguous. However, PEF detects the observed limit cycle only once: the regressions result mostly in stable dynamics. The estimates of  $m$  mostly confirm these selections (ambiguous results show intermediate values). For one data set of Veilleux, the ratio-dependent model is selected with OEF: these data show fast convergence to a sustained stable limit cycle with minima far above zero, a pattern that cannot be produced with the prey-dependent model. However, the fitted ratio-dependent model does not resemble the data very much. We think that this significant ratio-dependent fit results from the multiplicative error structure that gives more importance to points closer to zero. When repeating the regression assuming a Gaussian error, the fit becomes significantly prey dependent. See the Discussion for further remarks on Veilleux's data.

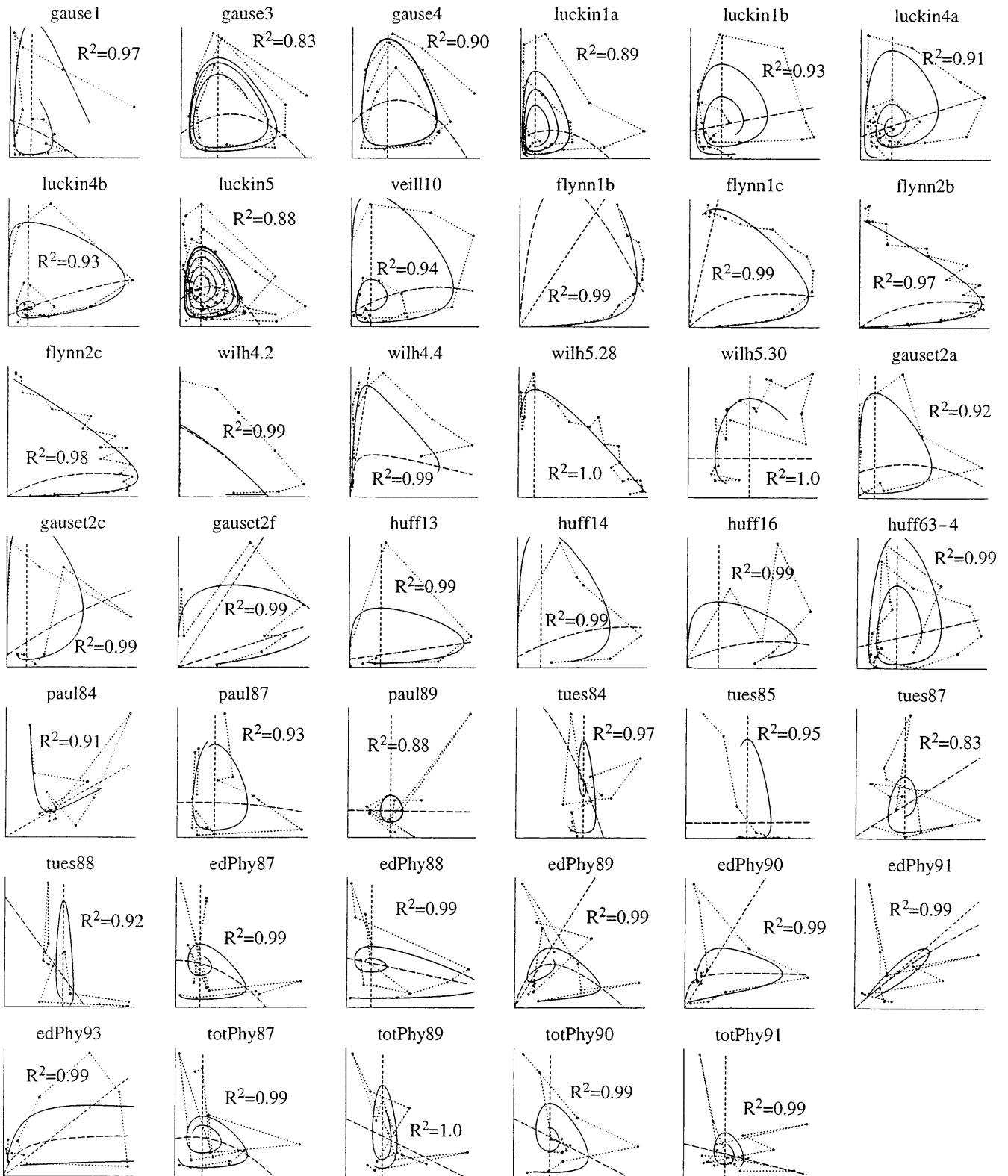
An interesting exception to this prey-dependent predominance is provided by the four data sets of Flynn and Davidson (1993): the ratio-dependent model is selected very significantly for all criteria and both types of fitting. Note that the estimates of  $m$  are all close to 0.5, indicating that the numerical value of this highly nonlinear parameter must be interpreted with caution (compare with dataset huff 16 with similar  $m$  but that fitted significantly better to the prey-dependent model).

The data of Wilhelm (1993) are the least conclusive: the prey-dependent and the ratio-dependent models are selected three times and one time, respectively, whereas two data sets yielded ambiguous selections. The preequilibrium dynamics in the time-series (always one large amplitude cycle followed by a long time of stable coexistence) are probably too short for a reliable model identification. The estimates of  $m$  are compatible with these selections (only the last dataset seems to show intermediate predator dependence).

## Mite data (spatially complex laboratory systems)

Both models fit rather poorly to Gause's and Huffaker's data on mites (low values of Eq. 3), causing numerous ambiguous results. The few significant results are always prey dependent, with one exception (gauset2f). The estimates of  $m$  confirm these selections with a tendency to being intermediate. All data show unstable oscillations that come close to extinction. These dynamics are correctly reproduced with both models and OEF (Figs. 3a, 4). Interestingly, the prey-dependent model retains these unstable dynamics with PEF while the ratio-dependent model mostly converges to a stable system; this is a further indication that the prey-dependent model is closer to the real dynamics.





**Fig. 4.** Representation of all significant OEFs in phase space (to facilitate comparison to Fig. 2). *Black dots connected by dotted lines* are the data; *black lines* are the fitted trajectories; *long dashed lines* are the prey isocline; *short dashed lines* are the predator isocline (*vertical in the prey-dependent model, slanted through the origin in the ratio-dependent model*)

## Plankton data (complex lake systems)

In general, the plankton data are very noisy and it is not clear if there are well-defined dynamic patterns or only noise. However, the algorithms seemed to find dynamic patterns in some cases.

With OEF, Paul Lake gives a significant fit four times, with two being prey dependent. PEF gives only one significant fit (prey dependent). Carpenter et al. (1994) had not found any significant result for this lake with discrete predator-prey models and PEF (one-step-ahead fitting), which agrees with our finding. The results are rather different in the manipulated Tuesday Lake. OEF selects the prey-dependent model in six of the seven time-series, with one ambiguity. PEF is less conclusive, selecting the prey-dependent model twice and the ratio-dependent model once, whereas three fits are nonacceptable and one is ambiguous. Interestingly, Carpenter et al. had found a good fit for this lake to the ratio-dependent model. We do not know if this discrepancy comes from the fact that we looked at seasonal dynamics or because we used continuous models.

In the case of Lake Geneva, prey data represent either edible algae only or total algal biomass. OEF gives the clearest trends: ratio dependent (four vs. two) for edible phytoplankton and prey dependent (six vs. one) for total phytoplankton. With PEF, the trends are less distinct but appear to contradict the previous results: prey dependent (five vs. zero) with edible phytoplankton and ratio dependent (three vs. two) with total phytoplankton. Ambiguities between results from the two types of fitting appear in two cases.

The  $m$  values are compatible with all model selections. Regarding the qualitative behavior, OEF often results in limit cycle behavior or the trajectories do not reach the stable equilibrium within one season (these fits are labeled transient in Table 2; see also Fig. 4). PEF nearly always results in stable systems; especially, the ratio-dependent model often shows strongly stable dynamics (a pattern termed limited predation by Arditi and Ginzburg 1989; see Fig. 2) where the equilibrium would be reached in less than 2 months.

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## Discussion

This study shows that predator-prey time-series can reveal the presence of predator dependence in the functional response if they are of good quality and show sufficient variation in predator abundance. The most significant results were obtained with the protozoan and plankton laboratory data. Most of these systems are closer to prey dependence. However, one predator-prey system with four time-series (Flynn and Davidson 1993) showed very significant predator dependence. The predators in this system are capable of strong interference in the form of cannibalism at low prey densities, although such cannibalism was not observed in the analyzed data (personal communication with the authors). Furthermore, the cultures were mixed only once per

day; therefore, the development of spatial heterogeneities was possible. Both factors have been shown to lead to predator dependence (Beddington 1975; Poggiale et al. 1998). To our knowledge, this is the first example of a marine plankton system with monospecific prey and predator that exhibits such strong predator dependence.

That simple homogeneous and monospecific predator-prey systems are better approximated by a prey-dependent model was also found by Kaunzinger and Morin (1998), studying the effects of enrichment in a three-level protozoan food chain, and by Bohannan and Lenski (1997, 1999), who reported that the dynamics and equilibria of a bacteria-bacteriophage system agreed better with a complex prey-dependent model than with a simple aggregated ratio-dependent model. Actually, microbiologists have a 40-year record of comparing the two functional responses (Eq. 2), although with a different vocabulary: the functional response corresponds to the substrate uptake function, the Holling type II model is known as the Monod model, and the ratio-dependent model (Eq. 2) is Contois' (1959) model. Reviewing this literature, Jost (2000) concluded that Monod's model seems adequate when the substrate is homogeneous and the microbial organism is a pure strain. In all other conditions (e.g., sewage or fermentation processes), substrate uptake is influenced by organism density, often to an extent that makes Contois' model more adequate than Monod's model.

The poor agreement between the long cyclic time-series of Veilleux (1979) and our simple models indicates that more complex models are necessary and justified with such high-quality data. Using additional time series from Veilleux (1976), Jost and Ellner (2000) reconstructed the functional response nonparametrically while also allowing for a delay in the reproduction functions of both prey and predator. Delayed effects not only improved the fit significantly but also revealed significant predator dependence in the reconstructed functional response (without delay, predator dependence did not show up). This predator dependence is, in most cases, very well approximated by the ratio-dependent model. This result suggests that the findings of the present study are only valid within our modeling framework, i.e., without delays.

There also seems to be little predator dependence in Gause's and Huffaker's mite data. In most cases, the prey-dependent model fits better or the time-series are too short to detect predator dependence reliably. Although most of the fits agree qualitatively with the data (see Figs. 3a, 4), Huffaker's data agree rather poorly from a quantitative point of view, which might be explained by his heterogeneous experimental setup. Such a laboratory system is structurally more complex than Gause's system or the protozoan batch cultures of the previous paragraphs.

The fits to phytoplankton and zooplankton data are the most difficult to interpret. Either the data are too noisy for this kind of model identification, or both models are too simple for lake dynamics. The first interpretation is supported by the fact that PEFs give mostly stable or strongly stable dynamics, suggesting that the best prediction is simply to use some mean abundance of prey and predator.

However, many significant model selections were obtained with OEFs, showing that long-term dynamic patterns exist. These significant fits are of both types (prey-dependent and ratio-dependent), with tendencies for some lakes: Tuesday Lake is (mostly) closer to the prey-dependent model, Lake Geneva with edible algae is closer to the ratio-dependent model, and Lake Geneva with total algal biomass is closer to the prey-dependent model. Brett and Goldman (1997) argued that the phytoplankton–zooplankton interaction is subject to both bottom-up and top-down forces, which might explain these differences among lakes. Recall also that we allowed for year-to-year differences in the physical environment but assumed the environment to be constant within a season. There is a growing literature that invokes seasonality (in temperature or light, for example) to explain plankton dynamics in lakes (see Scheffer 1998 for a recent review). Comparing our models to typical plankton dynamics (Sommer et al. 1986), we found elsewhere (see Chapter 4 in Jost 1998) that addition of a third trophic level (either top predators or nutrients) is another option to explain the distinct spring and summer peaks of phytoplankton. Our models might therefore be too simple for lakes and this drawback may cause the ambiguous model selections.

#### Model selection based on goodness-of-fit

How good are the fitting criteria in performing model selection? Considering the proportion of ambiguous model selections (marked with • in Table 2), we see that OEF was ambiguous half as often as PEF, in all analyzed systems. It appears therefore that OEF is a more efficient tool than PEF in selecting models; this difference was also noted by Harrison (1995). Polacheck et al. (1993) did a similar comparison between OEF and PEF with respect to parameter estimation and also favored the former due to the higher precision of the estimated parameters, just as we earlier found smaller parameter confidence intervals with OEF (Jost and Arditi 2000). However, the data contain both types of error, and Jost and Arditi (2000) showed that concurrent selection based on both types of fitting reduced the risk of a wrong selection by  $\approx 90\%$  compared to selection based on OEF only. Actually, model selection appears less limited by the type of fit than by the dynamic variation in relation to errors in the time-series. When there are strong dynamics over the whole length of the time-series, then both fits identify the same model; only if there is little dynamic variation (one large initial oscillation as in Wilhelm's data) or if the dynamics are hidden behind strong observation errors, as in lakes, do ambiguous results become more frequent.

Would we have obtained different results if we had based model selection on the estimates of  $m$  rather than on the goodness-of-fits of the two simpler models? With respect to the detection of predator dependence, little would change: ambiguous selections remain ambiguous; most selections are confirmed with a tendency to conclude intermediate predator dependence or not to select at all as a result of large parameter ranges. The algorithmic problems

(convergence) were more acute with the Hassell–Varley–Holling model. The most important observation is that the numerical value of  $m$  might give a wrong indication to practitioners who want to select a simple two-parameter model (see the Flynn and Davidson data or Huffaker's data).

A number of technical problems with both types of fitting are worth discussing. The strongest limitation of OEF is that it works only for relatively short time-series because process errors accumulate with time even in well-controlled laboratory systems (Harrison 1995). PEF is questionable with respect to the choice of  $s$  (time-steps-ahead prediction; see discussion in Ellner and Turchin 1995). However, compared with a preliminary analysis with  $s = 1$ , the present analysis only increased the number of significant selections without changing the selected model. Our conclusions thus appear to be quite robust with respect to the choice of  $s$ . A high potential for improvement can be found elsewhere: when predicting  $s$  steps ahead, our method implicitly also predicts 1, 2, . . . ,  $s - 1$  steps ahead, and there is currently no statistical solution for how this information should be properly incorporated into the fitting process (especially when fitting continuous models).

For future research in this direction, we also need more quantitative information on observation and process errors in the time-series data or more tests of the performance and selective power of algorithms which estimate them both simultaneously (Myers and Cadigan 1993; Bjørnstad et al. 1999); this would facilitate selection between models of different complexity (by using information criteria such as AIC or BIC; see Hilborn and Mangel 1997). However, these methods are computationally very expensive, especially for fitting continuous systems: bootstrapping one single data set can take a full week of computing time on a couple of workstations (Peter Turchin, personal communication). For such reasons, simpler regressions, as done in this article, will remain a useful tool in ecology, especially because extensive simulations with artificial data are often the only possibility to test whether the available data can answer the question at hand.

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## Conclusion

To summarize, well-controlled laboratory systems with monospecific prey and predators generally show little predator dependence in the functional response except in cases where predators have a strong potential to interfere with each other (e.g., cannibalism). However, this result seems to be valid only within the present modeling framework, because the inclusion of delays can have profound effects on the detection of predator dependence (Jost and Ellner 2000). More complex systems such as plankton in freshwater lakes show a multitude of patterns. These heterogeneous systems with multispecies prey and predator levels cannot be described by one simple type of functional response. Or, in the words of Yodzis (1994), "It remains frustratingly difficult to say just which functional form is the appropriate one for a given population." As a consequence,

population management decisions either should be based on statistical analyses that include this model uncertainty directly (Buckland et al. 1997; Wood and Thomas 1999) or they should be based on the predictions of several competing models, building up confidence in each model by constant comparison with actual observations. We should be comfortable if all models make the same prediction; otherwise, we must use the current level of confidence in a given model.

**Acknowledgments** We thank J.P. Pelletier and G. Balvay for kindly providing the data from Lake Geneva and helping with the data description. Special thanks go to A. Bar-Hen for long discussions on the statistical schemes and their appropriateness. We also thank G. Harrison for communicating the data set he had obtained from L. Luckinbill and S. Carpenter for kindly providing the raw plankton data on Paul and Tuesday Lakes. This research was supported by grants allocated to R.A. by the Swiss Priority Programme of the Environment (5001-034810), by the Swiss National Science Foundation (31-43440.95), and by the Programme “Environnement, vie et sociétés” of the French Centre National de la Recherche Scientifique. It was completed to a large extent while the authors were hosted at Université Paris-Sud XI, Orsay, France.

## Appendix A: Development of the stochastic model

Consider a process in the form of a simple differential equation (DE)  $dy/dt = f(y, \theta)$ , where  $\theta$  is a vector of  $q$  parameters. From this deterministic model, we construct a stochastic model that details how stochasticity enters the process and the observations of the state variable  $y$ . Based on this stochastic model, we can then develop the likelihood function to fit the DE to time-series data  $(t_i, Y_i)_{1 \leq i \leq n}$  (where  $t_i$  is the time at which the population  $y$  is observed to have density  $Y_i$  and  $n$  is the number of data points).

Let  $\hat{y}_i$  be the unknown real population density at time  $t_i$ , and  $y(t_i) = y(t_i, \theta)$  the deterministic solution of the differential equation at time  $t_i$  with parameters  $\theta$ . If there is only observation error in the data, then the whole trajectory is fitted (the process is deterministic) and there is only one initial condition,  $y(t_1) = \hat{y}_1$ , which is treated like a free parameter and estimated with the other parameters  $\theta$  (see Fig. 1a). If there is only process error, then the initial condition is different for each predicted data point and defined as the data point (measured without error)  $s$  steps previously,  $y(t_{i-s}) = Y_{i-s}$ ,  $s \geq 1$  (see Fig. 1b;  $s = 2$ ). With these notations and with  $\Delta t_i = t_i - t_{i-s}$ , the process can be written as follows:

Observation error $\omega$ only:	Process error $\nu$ only:
$\hat{y}_i = y(t_i, \theta)$	$\hat{y}_i = y(t_i, \theta)\nu(\Delta t_i, f, \theta)$
$Y_i = \hat{y}_i\omega$	$Y_i = \hat{y}_i$
$y(t_1) = \hat{y}_1$	$y(t_{i-s}) = Y_{i-s}$

Let us assume that observation error  $\omega$  and process error  $\nu$  are lognormal random variates with constant coefficients of variation  $CV_\omega$  and  $CV_\nu$ , respectively. Note that the accumulated process error  $\nu$  (best formulated by a stochastic differential equation) depends in general on the time interval between measurements and on the underlying process  $f$  with parameters  $\theta$ . To our knowledge, a better way of accounting for this process error in the fitting algorithm would

be computationally very expensive. Fortunately, the simulation analysis (Jost and Arditi 2000) (where the artificial time-series contained process error in the form of a stochastic differential equation) had shown that our gross simplification still gives fairly reliable model selection results, while allowing acceptable computing times (e.g., bootstrapping the estimates of  $m$  took 2 weeks on a fast iMac computer).

The log-transformed data are assumed to be Gaussian with expectation  $\log \hat{y}_i$  and standard deviation  $\sigma_\kappa = \sqrt{\log(CV_\kappa^2 + 1)}$ ,  $\kappa = \omega, \nu$ . Let  $r_i = \log Y_i - \log y(t_i, \theta)$  and  $V = \sigma_\kappa^2$  (note that, for vector-valued  $Y_i$ , the residual  $r_i$  is a vector and  $V$  is the variance-covariance matrix). With constant  $V$ , a maximum-likelihood fit of the model to the data is equivalent to minimizing the sum of squared residuals weighted by the variance-covariance matrix:

$$\chi_\kappa^2 = \min_\theta \sum_{i=1+s}^n r_i^T V^{-1} r_i, \quad \kappa = \omega, \nu \quad (4)$$

with  $s = 0$  for  $\kappa = \omega$ .

In our predator-prey model,  $Y = (N, P)$  and  $V = \begin{bmatrix} \sigma_N^2 & 0 \\ 0 & \sigma_P^2 \end{bmatrix}$ . In this case, Eq. 4 resolves to

$$\chi_\kappa^2 = \min_\theta \sum_{i=1+s}^n \left( \frac{(\log N_i - \log n(t_i, \theta))^2}{\sigma_N^2} + \frac{(\log P_i - \log p(t_i, \theta))^2}{\sigma_P^2} \right), \quad \kappa = \omega, \nu \quad (5)$$

For our data, the highest reported CVs were 0.5 (corresponding to  $\sigma = 0.47$ ), and little information was available on whether prey and predator variances were different. We thus assumed them to have the same value  $\sigma$ . With this assumption,  $\chi_\kappa^2$  is equivalent to standard least-squares regression in the case of observation error only (Press et al. 1992; Hilborn and Mangel 1997), whereas it is equivalent to conditional least-squares regression in the case of process error only (Dennis et al. 1995).

In general, the true nature of the error can be intermediate between Gaussian and log-normal; this was assumed in the regression analysis of Harrison (1995) performed with Luckinbill's data, but this approach requires another parameter that Harrison determined empirically. We refrained from such an approach for reasons of parsimony. The multiplicative error type appears overall better suited to the kind of data we analyzed.

For the Laplacian criterion, we assume that the log-transformed data have a double exponential distribution instead of a Gaussian one. Maximum likelihood with this error function results in the criterion

$$\chi_\kappa^L = \frac{1}{\sigma} \min_\theta \sum_{i=1+s}^n \left( |\log N_i - \log n(t_i, \theta)| + |\log P_i - \log p(t_i, \theta)| \right), \quad \kappa = \omega, \nu \quad (6)$$

Note that there now exist algorithms that permit estimating observation and process error simultaneously in the context of discrete time-series models (see Myers and Cadigan 1993 or Bjørnstad et al. 1999), but we could not find any information on how these algorithms perform for continuous models and in the context of model selection (where the estimated observation error should be independent of the underlying deterministic dynamic model, i.e., the same for all alternative models). However, we think that these algorithms have great potential for future research when higher computing power is available.

## Appendix B: Numerical methods, residual bootstrapping, and IE

The models were fitted to the time-series with error functions  $\chi_k^2$  and  $\chi_k^L$  in a three-step procedure: (1) computing upper and lower limits of the parameters from the time-series data, (2) finding starting values of the parameters with a genetic algorithm (GAlib 1.4.2 from <http://lancet.mit.edu/ga/>, with population size 50, mutation rate 0.01, crossover rate 0.1, and 600 generations), and (3) computing the optimal parameters with the downhill simplex method of Nelder and Mead combined with simulated annealing (routines `mrqmin` and `amotsa` from Press et al. 1992). See Jost and Arditi 2000 for a more detailed description. The solutions of the ordinary differential equations (needed to compute the error functions) were simulated with the adaptive step-size fifth-order Runge–Kutta method `odeint` from Press et al. (1992). In this regression scheme, we use only the available time-series data to estimate the parameters and, with them, the discrepancy between model and data. Only logical constraints such as positivity of parameters are applied. The genetic algorithm was mostly needed to obtain reasonable initial fits that permitted the other algorithms to converge without much manual work. Note that the fitting algorithm proposed in Bock (1983) might be an efficient alternative.

For residual bootstrapping, it is assumed that the model being used is correct and the parameters obtained by minimizing the equation  $\chi_k^2$  are used to construct the bootstrap time-series. The notation introduced in Appendix A is used. Fitting the whole trajectory (with initial condition as a free parameter or nuisance parameter) is related to simple nonlinear curve-fitting, and the following algorithm is taken from Efron and Tibshirani (1993). For PEF, the same algorithm can be used with some slight modifications that are indicated. Let  $\hat{\theta}$  be the best fitting solution to the original data, obtained by minimizing equation  $\chi_k^2$ , with the residuals

$$\hat{\varepsilon}_i = \log Y_i - \log y(t_i, \hat{\theta}), \quad 1 + s \leq i \leq n$$

( $s = 0$  for OEF) and total error  $\hat{e}$ . These residuals represent the empirical distribution function of the residuals. Then, the bootstrap estimates are created by the following algorithm:

1. For PEF only: fix initial values  $y_i^* = Y_i$ ,  $1 \leq i \leq n$ .
2. Calculate the bootstrap data  $(y_i^*)_{1+s \leq i \leq n}$  by

$$\log y_i^* = \log y(t_i, \hat{\theta}) + \varepsilon_i^* \quad 1 + s \leq i \leq n$$

where the  $\varepsilon_i^*$  are a random sample with replacement from the  $(\varepsilon_k)_{1+s \leq k \leq n}$  (for predator–prey data, all residuals are thrown in the same pool). For PEF,  $s \geq 1$  and the bootstrap data are calculated recursively.

3. Estimate  $\hat{\theta}^*$  from the bootstrap data by minimizing equation  $\chi_k^2$ , with final error  $e^*$ .
4. Go to the second step and repeat the loop  $B$  times ( $B = 50$ ).

Efron and Tibshirani (1993) suggested that  $B = 50$ – $200$  is in general sufficient for a reliable bootstrap estimate. Because regression of a differential equation to data is already quite costly, we used the lower value ( $B = 50$ ), thus permitting us to bootstrap one to four time-series per day. The standard deviations of the parameter  $m$  were estimated with  $B = 100$ .

With this bootstrapping procedure, we can compute the improved estimate of prediction error (IE; described in Efron and Tibshirani 1993, Chapter 17). Let  $e_{\hat{\theta}^*}$  be the error with the original data obtained using the fitted bootstrap parameters  $\hat{\theta}^*$ . The difference  $e_{\hat{\theta}^*} - e^*$  is in general positive and is called the “optimism.” The improved estimate of prediction error is now calculated by

$$IE = \frac{1}{n-s} \left[ \hat{e} + \frac{1}{B} \sum_{i=1}^B (e_{\hat{\theta}^*,i} - e_i^*) \right]$$

( $s = 0$  in the case of OEF), and its standard deviation is taken to be the standard deviation of the optimism scaled by the number of predicted data points. This estimation of prediction error is independent of the estimated residual variance and the number of parameters fitted; thus, it is less model dependent than alternatives such as  $C_p$  and  $BIC$  statistics (Efron and Tibshirani 1993).

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