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Restructuring Fundamental Predator-Prey Models by Recognising Prey-Dependent Conversion Efficiency and Mortality Rates



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Incorporating protozoa into population models (from simple predator-prey explorations to complex food web simulations) is of conceptual, ecological, and economic importance. From theoretical and empirical perspectives, we expose unappreciated complexity in the traditional predator-prey model structure and provide a parsimonious solution, especially for protistologists. We focus on how prey abundance alters two key components of models: predator conversion efficiency (e , the proportion of prey converted to predator, before mortality loss) and predator mortality (δ , the portion of the population lost though death). Using a well-established model system (*Paramecium* and *Didinium*), we collect data to parameterize a range of existing and novel population models that differ in the functional forms of e and δ . We then compare model simulations to an empirically obtained time-series of predator-prey population dynamics. The analysis indicates that prey-dependent e and δ should be considered when structuring population models and that both prey and predator biomass also vary with prey abundance. Both of these impact the ability of the model to predict population dynamics and, therefore, should be included in theoretical model evaluations and assessment of ecosystem dynamics associated with biomass flux.

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Introduction

Protozoa (heterotrophic protists) are primary consumers of prokaryotes and other protists across a wide range of natural and anthropogenic ecosystems: agricultural and natural soils; sewage

systems; endosymbionts within ruminants, amphibians, and insects; biofilms; marine and freshwater food webs; and aquaculture facilities. In these, protozoa act as mineralisers of material, sources of energy and material to symbionts and higher trophic levels, links that can alter ecosystem stability, controllers of alga blooms, and invasive species that can be detrimental to commercial productivity (Caron et al. 2009; Fenchel 1987; Kamra 2005; Parry 2004; Pauli et al. 2001). Understanding their

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population dynamics by developing and evaluating mechanistic models (i.e. those that are robust and informative) is, therefore, of considerable ecological and economic importance (Davidson 2014).

Protozoa are presently included in a range of numerical simulations, from large-scale predictive models of lake and ocean dynamics (e.g. Anderson et al. 2010; Kerimoglu et al. 2014; Schrum et al. 2006) to simple ones that explore fundamentals of structure and parameters (e.g. DeLong et al. 2014; Li et al. 2013; Montagnes et al. 2012). Regardless of their complexity, virtually all of these models incorporate the basic predator-prey structure central to the Lotka-Volterra equations; these describe prey (or victim, V) and predator (or consumer, C) population dynamics as:

$$\frac{dV}{dt} = V \times \text{prey specific growth rate} - C \times \text{functional response} \quad (1)$$

$$\frac{dC}{dt} = C \times [e \times \text{functional response} - \delta], \quad (2)$$

where the functional response is the predator *per capita* consumption rate in response to prey abundance, e is the efficiency of converting consumed prey into predator, and δ is the predator *per capita* death rate.

Over the years, the above structure has come under scrutiny, with some substantial improvement, but there remains a need to make models better. Here, we focus on an important issue that has received, surprisingly, little attention: how prey abundance alters predator conversion efficiency (e) and predator mortality rate (δ), two key parameters in Eq. 2. Based on the original Lotka-Volterra equations and traditional views (e.g. Calow 1977), in most models e is invariant with prey abundance, but recently Fenton et al. (2010) indicated that for protozoa e can vary considerably with prey abundance. Likewise, δ is typically assumed to be constant (and possibly negligible as protozoa are often thought of as “immortal”). Again this seems not to be so for protozoa; as prey become scarce mortality can increase exponentially (Minter et al. 2011).

Clearly, abiotic and biotic factors other than prey abundance (e.g. temperature, prey quality) will also influence e and δ , but the foundation of virtually all population models relies on prey-dependent rates (e.g. prey logistic growth, predator ingestion rate, as outlined by Eq. 1 and 2). Also, there will be interactive effects between prey-dependent rates and other factors (e.g. temperature-prey

interactions on gross growth efficiency, Kimmance et al. 2006). It, therefore, seems prudent to first establish mechanisms that account for the effects of prey abundance, before addressing confounding factors, such as temperature. Recognising this, here we assess the combined importance of prey-dependence on e and δ by comparing parameterised model simulations with observation of predator-prey dynamics, all examined on a single predator-prey system under a fixed set of conditions.

A text-book exemplar of a predator-prey system is that of the ciliates *Paramecium* (prey) and *Didinium* (predator). Notably used by Gause (1934a, b) to evaluate the recently established Lotka-Volterra predator-prey model, for almost a century these protozoa have been instrumental in both experimental and theoretical evaluation of species interactions (DeLong and Vasseur 2013; DeLong et al. 2014; Li et al. 2013).

Although, as mentioned above, Minter et al. (2011), using *Paramecium* and *Didinium*, proposed the need to consider prey-dependent mortality, and Fenton et al. (2010) argued that prey-dependent conversion efficiency should be included in protozoan-based models, they both examined their respective factor in isolation: the former assumed a constant e , and the latter assumed a constant δ . However, these two parameters can be intimately linked and may require concomitant evaluation (see Modelling Approaches).

Employing a combined experimental and theoretical approach with *Paramecium* and *Didinium* as our model system, we assess the interaction of prey-dependent δ and e and quantify the impact of changes in prey abundance on model interpretations and predictions. We do this by first imbedding prey-dependent δ and e into the commonly accepted, and routinely applied, Rosenzweig-MacArthur predator-prey model (see Modelling Approaches, below); our reason for this approach are twofold: 1) this process, didactically, provides clear evidence for the complexity of embedding prey-dependent δ and e into the existing structure, indicating that a new approach to constructing models may be required; and 2) there may remain cases where alternative approaches are not possible (e.g. re-examination of published models; cases where further data cannot be collected), so we outline means for modification of the Rosenzweig-MacArthur model to accommodate these cases. Through this process, we reveal that specifically for protozoa, and likely more generally, the Rosenzweig-MacArthur

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