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False Exclusion: A Case to Embed Predator Performance in Classical Population Models

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American Society of Naturalists,

RE, COVER LETTER and ASN GRANT-IN-NEED application

Dear ASN,

This submission is the final version of the manuscript 58702R3, "*False Exclusion: A Case to Embed Predator Performance in Classical Population Models*", by Montagnes et al.

I am applying for a *grant-in-need* that will cover the page charges and online-only appendix charges for a manuscript that has just been accepted but is not yet in production: 58702R3, "*False Exclusion: A Case to Embed Predator Performance in Classical Population Models*", by Montagnes et al.

Following your requirements for applying for this grant, I confirm that:

1) currently, I have no funds available to cover the Page Charges. My main co-author, Zhou Yang, has generously agreed to provide me with the $1000 for Open Access (needed by our institutions), but this has exhausted his funds. All the other Authors are either students or very junior researchers; they too have no funds available.
2) I am a fully paid up ASN member (Order Number: 7967905).
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Yours sincerely,

David Montagnes,

Dear Editor(s), our understanding is that there is no need for a "Response to Reviewers" at this point, as the manuscript "*False Exclusion: A Case to Embed Predator Performance in Classical Population Models*", by Montagnes *et al* has been accepted. We have, however, included a Cover letter, as requested.

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False Exclusion: A Case to Embed Predator Performance in Classical Population Models

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ABSTRACT

We argue that predator-prey dynamics, a cornerstone of ecology, can be driven by insufficiently-explored aspects of predator performance that are inherently prey-dependent: i.e., these have been falsely excluded. Classical -Lotka Volterra based- models tend to only consider prey-dependent ingestion rate. We highlight three other prey-dependent responses and provide empirically-derived functions to describe them. These functions introduce neglected nonlinearities and threshold behaviours into dynamic models leading to unexpected outcomes: specifically, as prey abundance increases predators: 1) become less efficient at using prey; 2) initially allocate resources towards survival and then allocate resources towards reproduction; and 3) are less likely to die. Based on experiments using model-zooplankton, we explore consequences of including these functions in the classical structure and show they alter qualitative and quantitative dynamics of an empirically-informed, generic predator-prey model. Through bifurcation analysis, our revised structure predicts: 1) predator extinctions, where the classical structure allows persistence; 2) predator survival, where the classical structure drives predators towards extinction; and 3) greater stability through smaller amplitude of cycles, relative to the classical structure. Then, by exploring parameter space, we show how these responses alter predictions of predator-prey stability and competition between predators. Based on our results, we suggest that classical assumptions about predator responses to prey abundance should be re-evaluated.

Introduction

Understanding population dynamics is central to virtually all ecological research, from theoretical explorations of species interactions, such as predator-driven extinctions and competition, to predictions of ecosystem function and stability. As predator-prey (or more generally consumer-resource) interactions are one of the main building-blocks of ecological models, it seems appropriate to include realistic aspects of predator and prey biology when they improve predictions; i.e., ignoring such aspects when they may have significant consequences constitutes “false-exclusion” (*sensu* Topping *et al*. 2015). To this end, age/size-structured and dynamic energy budget models have embraced complexity, providing better predictions and understanding of dynamics (e.g., De Roos *et al*. 2008, Nibet *et al*. 2010). However, parametrising these models can be difficult or impossible, and for multi-trophic level models including such complexity is unlikely to be computationally pragmatic. Consequently, performance at the individual level (i.e., *per capita* responses) is often translated to generalities that are then applied at population and community levels, based on the classic Lotka-Volterra structure (Turchin 2003; Begon *et al*. 2012). For instance, in classical population models the shape of functional response may be considered sigmoidal rather than hyperbolic (e.g., Jeschke *et al*. 2002); predator-prey ratio-dependence may be included (Arditi and Ginzburg 2012); and delayed density-dependence may be imposed on prey and predator *per capita* rates (e.g., Turchin 2003; Li *et al*. 2013). Likewise, functional complexity in how predators allocate energy to maintenance and reproduction has been incorporated into classical model structures, often even at the expense of parsimony (Topping *et al*. 2015). In this sense, dynamic energy budget theory that focuses on the partitioning of individual resources (Kooijman 2010) has improved more traditional models. There, thus, is a long history of elaborating on the classical structure by including more realistic predator-responses, driven by better understanding and appreciation of their biology.

A revised consumer-resource model

Here, we explore aspects of predator biology that have largely been "falsely excluded": prey-dependent conversion efficiency, birth rate, and death rate. In doing so, we address previously recognised yet nevertheless unresolved issues associated with how aspects of *per capita* performance are currently viewed and applied in classical population models. As a relevant and translational example of predators, we focus on zooplankton (e.g., Carlotti *et al*. 2000; Tian 2006). By employing these "model animals", we empirically explore the above prey-dependent responses and in doing so generalize the classical population model structure to ask what happens if classical assumptions regarding predator performance are relaxed.

A revision of the classical predator-prey model

Most classical models of predator (consumer, C) - prey (resource, R) dynamics ultimately rely on two linked equations, based on a framework established ~100 years ago by Lotka and Volterra (see Turchin 2003). In this structure prey population growth (Eq. 1) is determined by their prey-dependent specific growth rate (μ), and prey loss occurs when they are consumed by the predator. Only the ingestion rate (I) is prey-dependent; i.e., the functional response, $I = f_I(R)$. Predator population growth (Eq. 2) is then determined by assuming that the gross increase (typically termed "births", b) is a fixed proportion (e) of the ingested prey, and loss of predators is by prey-independent deaths (d).

$$\frac{dR}{dt} = \mu R - f_I(R)C \tag{1}$$

$$\frac{dC}{dt} = C[ef_I(R) - d] \tag{2}$$

Therefore, in the classical framework, predator *per capita* growth rate (r, Eq. 3a), which ultimately depends on the predator's birth (b) and death (d) rates, is obtained indirectly through the predator's ingestion rate (Eq. 3b). Neither the *per capita* growth nor birth rate is explicitly parameterised. Rather, b is obtained indirectly, assuming that a proportion of the prey that is ingested contributes to an increase in predator numbers, and a finite proportion of the ingested prey (I_τ) is allocated to survival. Implicitly, then, ingestion leads to births, but new individuals are only produced when $I > I_\tau$; i.e., birth rate (b) is greater than death rate (d), and specific growth rate ($r = b - d$) is positive. Conversely, when $I < I_\tau$, growth rate is negative, and the population declines. Note that above (and below) we discuss populations in terms of numbers (i.e., abundance per area or volume). Although some models replace numbers with biomass, we have chosen the former as it tends to facilitate intuitive understanding of population dynamics.

In this widely accepted structure (e.g., as reviewed by Turchin 2003; Arditi and Ginzburg 2012; Begon *et al*. 2012), the proportion of ingested prey that contributes to an increase in predators (i.e., the conversion efficiency, e) can then be obtained from the ratio of two constants ($e = d_0 / I_\tau$), where d_0 is the *per capita* predator death rate in the absence of prey (Eq. 3b). Hence,

$$\frac{dC}{dt}\frac{1}{C} = b - d_0 = r \tag{3a}$$

or,

$$\frac{dC}{dt}\frac{1}{C} = e(I - I_\tau) = \frac{d_0}{I_\tau}I - \frac{d_0}{I_\tau}I_\tau \tag{3b}$$

To appreciate why $e = d_0 / I_\tau$, consider the case where the amount of ingested prey just allows survival ($I = I_\tau$); at this point through substitution $b = d_0$ (Eq. 3a,b), and growth rate is zero ($r = 0$). Likewise, when no prey is available (i.e., $R = 0$) ingestion must be zero ($I = 0$), growth rate will be negative, and $-r = d_0$. Thus, for the classical framework, by determining predator death rate in the absence of prey (d_0) and the ingestion rate at the prey level where predators just survive (I_τ), conversion efficiency (e) can be obtained, and birth rate can be predicted ($b = eI$). The mathematical elegance and experimental practicality of this structure (Eq. 1, 2) provides a means to obtain all the required parameters. Moreover, the equations lend themselves to analytical solutions, even when the structure is made more realistic (e.g., the Rosenzweig-MacArthur predator-prey structure, see below). This has facilitated the generation of an extensive body of literature that has explored model predictions, for conditions ranging from simple consumer-resource to complex multi-trophic systems.

Here we suggest that insufficient representation of predators in models based on the above classical structure (Eq. 2) may yield misleading qualitative and quantitative predictions, and hence constitutes false exclusion. This is because, although appealingly tractable, Eq. 3b is not grounded on sound biology. It fails to account for three aspects of predator performance that may alter model predictions: 1) predators become inefficient in their processing of captured prey as prey become more available (e.g., Fenton *et al*. 2010; Montagnes and Fenton 2012); 2) predators initially prioritise resource allocation towards survival, and then as food availability increases they allocate resources towards reproduction (e.g., Kooijman 2010); and 3) predators are less likely to die as resources become more available (e.g., Heller 1978; Minter *et al*. 2011). At least for protozoa, including these improves the ability of the classical structure to predict empirically observed predator-prey cycles (Li and Montagnes 2015). However, the above aspects of performance are rarely fully characterised (i.e., their theory requires elucidation), and much of their empirical exploration has relied only on protozoan-based studies, rather than animal-studies (e.g., Fenton *et al*. 2010, Minter *et al*. 2011, Li and Montagnes 2015). -Although protozoa are in many ways ideal model organisms, they may not capture aspects of tissue- and organ-level processes expressed by animals (Montagnes *et al*. 2012)- Consequently, the individual and combined roles of these three responses in classical population models has not been appreciated.

We first review past predictions that incorporate the above aspects of predator performance and offer a revised structure for Eq. 2. This new framework accounts for prey-dependent allocation of resources, through conversion efficiency, leading to changes in starvation, survival, and births. We then present evidence to support the contention that this revised "resource allocation" framework yields new and potentially important insights; i.e., using zooplankton, we reveal how the interaction of these responses may produce different and likely more realistic representation of predation. Finally, through empirically-informed sensitivity analysis, we explore how predator-prey dynamics and competition between predators might be affected by the revised structure.

Three issues: appreciating prey-dependent resource allocation

First we support past arguments and observations that "assimilation efficiency" ($\varepsilon = [I\text{-}E]/I$, where I is ingestion and E is egestion), and, therefore, conversion efficiency (e) should decrease with increasing prey availability (Fig. 1a-e). Both physiological and methodological explanations exist for this decrease: 1) with increased prey abundance the rate of materials transported across the gut wall (i.e., assimilation) may be reduced, and gut passage rate may increase (Calow 1977; Straile 1997; Jumars 2000; Mitra and Flynn 2007; Flynn 2009) and 2) measures of ingestion (I) often reflect loss from the prey population rather than ingestion *per se*; i.e., prey may be killed but not ingested. This "wasteful" or "surplus-killing" can increase with prey abundance (Johnson *et al*. 1975; Sih 1980; Mckee *et al*. 1997; Straile 1997; Riechert and Maupin 1998; Lang and Gsödl 2003, Turchin 2003; Appleby and Smith 2018; Veselý *et al*. 2018). Either of these processes, which are exhibited by a wide range of animals, violate the assumption that e is constant (i.e., d_0/ I_τ, Eq. 3b). Rather, we can predict that e will decrease with increasing prey abundance (e.g., Fig. 1b-e, 2e short-dashed line), although we note that arguments have been made that e may also increase with prey abundance (e.g. Fenton *et al*. 2010).

Second, many animals prioritise resources for individual survival (maintenance and somatic growth), and only after these needs are met will they allocate further resources to reproduction (Zera and Harshman 2001; Lika and Kooijman 2003; Speakman 2008; Kooijman 2010). This organism-level of energy allocation can be applied to *per capita* rates used in population models, and Eq. 2b can then be revised such that below a threshold ingestion rate (I_β, occurring at the prey abundance R_β, Fig. 2b) the production of individuals (b) ceases, and energy is allocated only to maintenance; i.e., b vs R is a function with a discontinuous first derivative, with $b = 0$ for $I \leq I_\beta$. In contrast to what was implied above (see Eq. 3b), I_τ (occurring at the prey concentration R_τ, Fig. 2d) is not the ingestion rate that allows the predator to just survive (i.e., $b = d$); rather it combines the ingestion rate needed for survival plus that needed to produce new individuals (I_β). Critically, recognising, and applying, the existence of I_β (and hence R_β, Fig. 2b) alters the above prediction that e decreases monotonically with prey availability (Fig. 1b-e, Fig. 2e short-dashed line). Rather, as $I \rightarrow I_\beta$, $e \rightarrow 0$. Then as I increases above I_β, e will increase towards an asymptote, or e will reach a maximum and subsequently decrease, assuming the above arguments regarding assimilation and wasteful killing apply (Fig. 1a, 2e solid and long-dashed lines). Consequently, we can now predict that e vs R is a unimodal function with a discontinuous first derivative, whereby $e = 0$ for $I \leq I_\beta$ (at prey abundance = R_β) and -when based on biomass rather than abundance- ranges between 0 and 1 for $I \geq I_\beta$ (Fig. 2e solid and long-dashed lines). For our subsequent analysis (see *Developing a framework for prey-dependent resource allocation*) there are important implications if $R_\beta : R_\tau$ is large (i.e., approaches 1). Here, and more generally (e.g., Bayliss and Choquenot 2002; Tian 2006; Fenton *et al*. 2010), studies assume that the numerical response, $f_r(R)$, is smooth (Fig. 2d short-dashed line), represented by a rectangular hyperbolic function with a non-zero intercept (this is detailed, later, see Eq. 6, R_τ). However, where resources needed to produce new individuals is large compared to those needed to survive (i.e., when $R_\beta : R_\tau$ is large) this is not so: the numerical response will be composed of two apparently saturating curves, forming a complex function (Fig. 2d long-dashed line). Below we argue that when $R_\beta : R_\tau$ is small (e.g., Fig. 2 b,d,e solid line), the numerical response (Fig. 2 d) can be approximated by a rectangular hyperbolic function (Eq. 6, see *Developing a framework for implementing prey-dependent resource allocation* and the Discussion).

Third, animal health and longevity are reduced when food is scarce (McCauley *et al*. 1990; Carlotti *et al*. 2000; Lochmiller and Deerenberg 2000; Minter *et al*. 2011). It then follows that death rate will decrease with increasing prey availability (Fig. 1 f-j; Ginzburg 1998, Tian 2006), providing another violation of the logic on which the classical structure (Eq. 2b) is based; i.e., d is not a constant. Therefore, in the absence of prey, predator death rate (d) will be at its maximum (i.e., d_0, Eq. 3), but as prey become more available increased nourishment will reduce the likelihood of death (Fig. 2c). Empirical data support this trend (Fig. 1 f-j), but for thoroughness we note that death rate may increase with fecundity (Veselý *et al*. 2017), and ageing (and hence mortality) may increase with increased caloric intake, even in zooplankton (Saiz *et al*. 2015). As both fecundity and caloric intake may increase with prey abundance, the mechanistic basis for the observed decline in mortality with increasing prey abundance is unlikely to be simple and bears further investigation, beyond the scope of this study. Instead, below, we provide a phenomenological function for predicting death rate.

Developing a framework for implementing prey-dependent resource allocation

We now explore how the biological realism presented above can be implemented in the current classical structure (Eq. 1, 2). To do so, we employ the Rosenzweig-MacArthur predator-prey model (Eq. 4, 5), being a common elaboration that embraces additional reality (Turchin 2003; Arditi and Ginzburg 2012). Here, prey growth is logistic (with carrying capacity, K, Eq. 4a) and predator ingestion follows a Type II functional response (with a maximum ingestion rate I_{MAX} and a half saturation constant k, Fig. 2a; Eq. 4b). Predator growth follows the classical framework (Eq. 2), where births are the product of a constant conversion efficiency (e) and ingestion rate (I), and death rate (d_0) is constant (Eq. 5a). This structure can then be modified to better reflect the energy allocation described above by including prey-dependent conversion efficiency and death functions, $f_e(R)$ and $f_d(R)$, respectively (Eq. 5b).

$$\frac{dR}{dt} = \mu R\left(1 - \frac{R}{K}\right) - Cf_I(R) \tag{4a}$$

$$f_I(R) = \frac{I_{\mathrm{MAX}}R}{k+R} \tag{4b}$$

$$\frac{dC}{dt} = C\left(e\frac{I_{\mathrm{MAX}}R}{k+R} - d_0\right) = Cr \tag{5a}$$

$$\frac{dC}{dt} = C\left(f_e(R)\frac{I_{\mathrm{MAX}}R}{k+R} - f_d(R)\right) \tag{5b}$$

How then might $f_e(R)$ and $f_d(R)$ be obtained, so that we can explore the impact of these prey-dependent responses on predator-prey dynamics? Since the seminal work of Holling (1959) numerous methods have been developed to determine the functional response (Eq. 4b). Likewise, the loss of individuals from a population, and hence $f_d(R)$, may be feasibly estimated in the field or laboratory (e.g., Krebs 1989; Minter *et al*. 2011, references cited in Fig. 1). However, few methods exist for directly measuring prey-dependent e (Fenton *et al*. 2010). As we show that $e = b/I$, it follows that $f_e(R)$ can be calculated as $f_b(R) / f_I(R)$. Determining the numerator, the gross increase in individuals (b, which is rarely equivalent to "births" *per se*, as new-borns may die before becoming functionally active), is possible (e.g., long-lived vertebrates) but may be challenging, especially for smaller animals such as zooplankton. In contrast, it is often relatively simple to measure prey-dependent specific growth rate (i.e., r, the net change in individuals), providing $f_r(R)$, including negative rates at low prey levels (e.g., Fenton *et al*. 2010). Then, as $r = b - d$, if $f_r(R)$ and $f_d(R)$ are known it follows that $f_b(R)$ can be obtained. Our model animals lend themselves to this approach, and the analysis that we propose relies on predicting $f_b(R)$ and $f_e(R)$, with the recognition that R_β is small and the numerical response can be approximated by Eq. 6 (see *Three issues: appreciating prey-dependent resource allocation*).

Our logic is based on bioenergetics arguments where *r* is a function of ingestion (Ginzburg 1998), and thus the numerical response will reflect the functional response (Fig. 2a,d, Fenton *et al*. 2010); here growth rate reaches an asymptote (r_{MAX}) and the initial curvature of the response is described by k_2 (Eq. 6).

$$f_r(R) = \frac{r_{\mathrm{MAX}}(R - R_\tau)}{k_2 + R - R_\tau} \quad (6)$$

The main distinction between the functional (Eq. 4b) and numerical (Eq. 6) responses is that the latter has a positive *R*-intercept (i.e., a threshold prey abundance, R_τ) where ingestion (I_τ) accounts for maintenance and reproductive costs (Fig. 2d). A difference in shape between the numerical and functional responses implies that *b* and/or *d* are prey-dependent (Fenton *et al*. 2010). Once the numerical response is established, determining the response of *d* to prey abundance (i.e., a mortality response, Fig. 1f-j, Fig. 2c) provides the relation between *b* (and hence *e*) and prey abundance (Fig. 2e).

For years, work on model organisms such as the water flea *Daphnia*, rotifers, and protozoa has provided valuable insights into more general predator performance (e.g., as reviewed by Gause 1934 and Kooijman 2010). Initial work on protozoa has recognised a need to assess prey-dependent predator responses (Minter *et al*. 2011; Li and Montagnes 2015) and suggests that including these responses improves model predictability (Li and Montagnes 2015). Here, we apply our revised prey-dependent resource allocation structure (Eq. 5b) to several model predators from both marine and freshwater habitats, covering a range of lineages (i.e., two rotifers, two cladocerans, one protozoan), with a view to reveal general trends for zooplankton and argue for their wider adoption. Notably, this is the first time that prey-dependent growth, ingestion, and death rates have been examined concurrently on single predator-species. These unique, empirically derived data and the responses that arise from them can then reveal the potential impact of $f_e(R)$ and $f_d(R)$ on predator-prey dynamics.

Materials and Methods

Study organisms, maintenance, and experimental conditions

Four model animals (the rotifers *Brachionus calyciflorus* and *Brachionus plicatilis* and the cladocerans *Moina macrocopa* and *Daphnia magna*) and the model protozoan *Didinium nasutum* were grown on prey at a range of concentrations (see Fig. 3). Cultures were grown under standard, constant conditions: *B. calyciflorus* was maintained in purified natural spring water containing the alga *Chlorella vulgaris*, cultured in Bold's basal medium (Sigma Aldrich, UK) at 50 µmoles m^2 s^{-1} (light:dark, 18:6 h) and 21 °C; *B. plicatilis* was maintained in artificial seawater containing the marine algae *Chlorella* sp. or *Phaeocystis globosa*, cultured in f/2 medium (Sigma Aldrich, UK); *D. magna* and *M. macrocopa* were maintained in purified natural spring water containing the freshwater alga *Chlorella* sp., cultured in BG-11 medium (Sigma Aldrich, UK); *D. nasutum* was maintained in purified natural spring water containing the ciliate *Paramecium caudatum*, cultured on the bacterium *Aeromonas sobria. Chlorella* sp. (marine and freshwater) and *P. globosa* were grown at 50 µmoles m^2 s^{-1} (light:dark, 12:12 h) and 25 °C. Experiments on *B. plicatilis, D. magna, M. macrocopa*, and *D. nasutum* were conducted at 25 °C. Predator abundance and *P. caudatum* abundance were determined by microscopy. Autotrophic prey abundance was determined by fluorometric-methods, standardized by microscopy. For all experiments prey were harvested in exponential phase, ensuring consistency in their nutritional content. All experiments were conducted at relatively low and constant predator abundances, removing the potential for bias due to predator-interference (for further details see Appendix 1).

A revised consumer-resource model

Functional, numerical, mortality, and conversion efficiency responses

For all rate measurements, predators were acclimated to defined prey concentrations for ≥ 48 h prior to the experiment. For autotrophic prey, ingestion rate (I, prey predator^{-1} d^{-1}) was measured by observing the depletion of prey. For ingestion of *P. caudatum* by *D. nasutum*, methods followed those described by Li and Montagnes (2015), where *P. caudatum* were fed fluorescent beads, and then *D. nasutum* that had ingested prey could be detected. For all ingestion rates, a defined number of randomly selected predators, chosen to represent the typical population structure and covering the range of developmental stages (to obviate size-related biases), were placed in a container, in the dark, with prey at a defined abundance. For the metazoa, I was determined as the linear decrease in prey abundance over an appropriately short period, depending on the concentration (< 2 h); controls containing only prey indicated no prey growth. For the protozoan, I was determined as the increase in predators containing prey over an appropriate period, depending on the concentration (< 30 min).

Growth rate measurements were based on the widely applied methods (Montagnes 1996). Predator growth rate (r, d^{-1}) was determined on initial numbers of 10 to 80 (for the animals) and 2 to 30 (for the protozoan). Initial numbers depended on the prey concentration, as at low prey levels the predator numbers decreased (i.e., negative growth rate). Predators were randomly chosen, covering the range of developmental stages (to obviate the need to assess age-specific growth rates). Predators were placed in a container filled with prey at a target concentration. After 24 h predator numbers were determined. For the animals, all individuals were then transferred to a new container with fresh prey, at the target prey concentration. For *Didinium*, where growth was positive, only two individuals were chosen. This process maintained predators at a constant prey level and was repeated for 4 to 5 days. For the animals r was then calculated by regressing *ln* abundance against time, over the incubation, while for *Didinium*, r was determined each day and the average was calculated.

Death rate was determined by applying methods established for small organisms (Minter *et al*. 2011): in brief, predators were individually isolated in several containers (~50 isolates per prey concentration), each filled with prey at a single defined concentration; this process was repeated for each prey level. Again, predators were randomly chosen, covering the range of developmental stages (to obviate the need to assess age-specific death rates). Every 24 h, for 5 to 6 d, individual predator survival/death was observed, and each day the original, surviving individuals were moved to new containers at the same target prey concentration; i.e., if numbers increased due to parthenogenic reproduction (for all animals), only the adult was retained and transferred, and when the protozoan predator increased by clonal growth one randomly chosen individual was retained. Death rate was then determined by regressing the decrease in *ln* abundance of original isolates (i.e., containers remaining occupied) against time. The mortality response was represented by Eq. 7, which embraces features exhibited by the change in death rate with prey abundance and reflects trends observed by us and elsewhere (e.g., Fig. 1 f-j, see Results),

$$f_d(R) = \frac{\alpha k_\delta}{k_\delta + R} + d_{\mathrm{MIN}} \tag{7}$$

where d_{MIN} is the minimum death rate (d^{-1}) at saturating prey, $\alpha + d_{\mathrm{MIN}} = d_0$, and k_δ defines the curvature of the response.

For all experiments, effort was placed on collecting rate measurements across the breadth of prey concentrations, with more measurements at low levels and no replication (Montagnes and Berges 2004). Prey abundances were determined as the average prey level over each incubation; consequently there are differences in the prey concentrations examined between responses. Functional (Eq. 4b), numerical (Eq. 6), and mortality (Eq. 7), responses were fit to the data using the Marquardt-Levenberg algorithm, which is appropriate for such data (Berges *et al*. 1994). Standard errors of the estimates and R^2 values were obtained, as indications of goodness of fit.

A revised consumer-resource model

Prey-dependent birth rate, $f_b(R)$, and conversion efficiency, $f_e(R)$, responses were obtained from the above functional, numerical, and mortality responses. As $b = r + d$, $f_b(R)$ was determined from the $f_r(R)$ and $f_d(R)$, with the caveat that $R_\beta : R_\tau$ is relatively small (see *Three issues: appreciating prey-dependent resource allocation*). Although e may be presented in terms of prey and predator abundance, it is more intuitively understood in terms of biomass, with the latter ranging from 0 (100% inefficient) to 1 (100% efficient). As abundance based $e = b/I$, the response of biomass-based conversion efficiency to prey abundance was determined by Eq. 8,

$$f_e(R) = [f_r(R)M_c + f_d(R)M_c] \,/\, [f_I(R)\, M_R], \qquad (8)$$

where M_C and M_R are the individual biomass of the predator and prey, respectively (Table 1).

Model exploration

Analysis of population dynamics involved numerical simulations, as determining analytical solutions was not possible, due to the discontinuities in responses; i.e., following Eq. 4a and 5a or 4a and 5b (as outlined below), under any one set of conditions (e.g., a defined carrying capacity), a numerical simulation was run until steady-state population dynamics arose (i.e., equilibria or constant cycles), and then values of variables (e.g. maximum and minimum abundances of cycles) were obtained. To explore how population dynamics responded to changing conditions, parameters (e.g. carrying capacity, curvature of the mortality function) were varied through a range of biologically realistic values, informed by our empirically-derived data and published data on planktonic systems (e.g. Fig. 1, Fig. 3; Berges *et al*. 1994; Montagnes *et al*. 1996; Båmstedt *et al*. 2000; Besiktepe and Dam 2002; Kimmance *et al*. 2006; Fenton *et al*. 2010; Minter *et al*. 2011; Montagnes and Fenton 2012; Yang *et al*. 2013; Li and Montagens 2015). To reveal trends, numerous simulations were performed across the varied parameter; as the solutions were not analytical, inevitably, these trends are rarely perfectly smooth response, but they are indicative and proved to be sufficient for revealing differences.

Model evaluations were based on a generic predator (Table 1) and a generic prey (μ = 1.0 d^{-1}, $K = 10^6$ ml^{-1}), as above both reflecting our observed trends (Fig. 3, Table 1) and those from the literature. Abundance-based predator-prey dynamics either followed the classical structure (i.e., the Rosenzweig-MacArthur model, Eq. 4a, 5a) with constant values of d_0 and e, or they followed our revised, resource allocation structure (Eq. 4a, 5b, Table 1). For the latter, $f_d(R)$ followed Eq. 7, and $f_e(R)$ was obtained from $f_I(R)$, $f_r(R)$, and $f_d(R)$, as outlined above in *Developing a framework for implementing prey-dependent resource allocation* (see Table 1 "Generic Predator" for parameters for $f_I(R)$, $f_r(R)$, and $f_d(R)$ and Fig. 3 for a visual presentation of these functions). For the classical structure, values for a constant death (d_0) and constant conversion efficiency (e) were obtained as follows. First, $d_0 = \alpha + d_{MIN}$ (Eq. 7, where α and d_{MIN} are presented in Table 1). Then to determine e we followed logic outlined in *A revision of the classical predator-prey model*: *i.* R_τ was first obtained from numerical response (Generic Predator, Table 1); *ii.* then from the functional response (Generic Predator, Table 1) we obtained I_τ; and finally, *iii.* $e = d_0/ I_\tau$ (Eq. 3b).

Through these simulations we address three issues associated with how prey-dependent conversion efficiency, $f_e(R)$, and death rate, $f_d(R)$, may alter model predictions of dynamics. Firstly, to assess differences between responses of the two structures, we performed a bifurcation analysis, to compare the influence of increased prey carrying capacity (K) on predator extinction, predator-prey equilibrium, and the magnitude of limit cycles. In this analysis four cases were examined: 1) e and d_0 were constant (i.e., the classical structure); 2) both $f_e(R)$ and $f_d(R)$ were included (i.e., our revised resource allocation structure); and 3) and 4) only $f_e(R)$ or $f_d(R)$ was included, and, respectively, a constant d_0 or e was included (i.e., a combination of the two structures, to isolate the effects of $f_e(R)$ and $f_d(R)$). Secondly, recognising distinct differences between predictions of the two structures (see Results), we conducted a stability analysis on the resource allocation structure, to assess the influence of changing parameters of $f_e(R)$ and $f_d(R)$, over realistic ranges of their responses to prey abundance (based on observations from empirical data): specifically, the curvature of the mortality response was varied by increasing k_δ, and the shape of the conversion efficiency response was altered by increasing R_τ, effectively increasing R_β (Fig. 5a,b). Thirdly, to extend the analysis to evaluate predator competition -a realistic aspect of predator-prey dynamics- and to further assess the effect of prey-dependent *e* and *d*, when one response remains invariant, we assessed the extent to which differences in $f_e(R)$ and $f_d(R)$ will alter the competitive advantage between two predators (C_1 and C_2) offered a single-prey, when one predator exhibits superior levels of *e* and *d*. Here, we applied an additive model of exploitative competition, such that each predator acted independently of the other with interaction only being indirect, via the limiting prey resource. Eq. 9 and 10 describe the model, where all parameters are defined above, and the subscripts *i* represents the superior (C_1) and inferior (C_2) competing predators. Only death rate, $f_{d2}(R)$, or conversion efficiency, $f_{e2}(R)$, responses of C_2 were altered (as described in Fig. 5a,b).

$$\frac{dR}{dt} = R\mu\left(1-\frac{R}{K}\right) - C_1\frac{I_{\mathrm{MAX}}R}{k+R} - C_2\frac{I_{\mathrm{MAX}}R}{k+R} \tag{9}$$

$$\frac{dC_i}{dt} = C_i\left(f_{ei}(R)\frac{I_{\mathrm{MAX}}R}{k+R} - f_{di}(R)\right) \tag{10}$$

The competition model was initiated with 1 of each predator ml^{-1}. To quantify the change in competitive success with respect to altered conversion efficiency and death rate (see Fig 5a,b), we determined the time for the inferior predator (C_2) to reach an abundance at which it was considered to be functionally extinct, $<10^{-2}$ ml^{-1}.

Results

Prey-dependent responses

The predator responses reveal consistent prey-dependent trends across our model taxa (Fig. 3 columns 1-6), following those predicted by our revised theory (cf. Fig. 2 vs Fig. 3). Data underlying figure 3 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.674p6n0 (Montagnes *et al*. 2019). Ingestion and specific growth rates followed typical "Type II" (Eq. 4b, Eq. 6), asymptotic responses (Fig. 2a,d; Fig. 3, rows 1 and 2, respectively, Appendix 2), with the latter having a positive *R*-intercept (i.e., a growth threshold prey concentration, R_τ). For all taxa death rates (*d*) followed the predicted trend (Fig, 2c, Eq. 7), being maximal when prey were absent and then decreasing towards a minimum with increasing prey abundance (Fig. 3, row 3). Prey-dependent birth rate (Fig. 3, row 4), i.e., $f_b(R) = f_r(R) + f_d(R)$, followed the predicted (Fig. 2b) asymptotic response with a non-zero *R*-intercept (R_β), below which *b* was zero. Values of $R_\beta : R_\tau$ were < 1 (Table 1), validating our assumption that Eq. 5 could be applied to approximate prey-dependent *b* and *e* responses (see *Three issues: appreciating prey-dependent resource allocation*). Biomass-based predator conversion efficiency (*e*; Fig. 3, row 5; Eq. 8) followed the predicted trend (Fig. 2e), rapidly increasing from zero at R_β to a maximum that was relatively consistent across responses (0.1 - 0.3), and then decreasing as prey abundance increased; the one exception was *Brachionus plicatilis* fed the poor-quality *Phaeocystis globose*, where there was no observable initial increase in *e* (Fig. 3xv). Critically, the predicted non-linear responses of *b*, *d*, and *e* would not have been detected if assumptions associated with the classical model structure (Eq. 4a, 5a) had been applied to assess performance.

Model exploration

The resource allocation framework (Eq. 4a, 5b) generated distinctly different dynamics to those of the classical framework (Eq. 4a, 5a), as carrying capacity was increased (Fig. 4a-f). When both prey-dependent *e* and *d* were included and compared to the classical model (Fig. 4a,b): 1) the classical model predicted that the predator persisted when the prey carrying capacities (*K*) was half that required for persistence by the resource allocation model; 2) for both the predator and the prey, the resource allocation model predictions were more stable than those of the classical model, producing stable equilibrium dynamics over more than twice the range of prey carrying capacities, and for the predator a ~20 times lower amplitude of limit cycles, when they occurred; and 3) the classical model predicted that cycles drove the predator to extinction (i.e., $<10^{-2}$ ml^{-1}) at prey carrying capacities > 3.2 x 10^{6} ml^{-1}, whereas for the resource allocation simulations the predator remained extant over the entire range examined. When only prey-dependent *e* or *d* were included in simulations, the above differences also occurred but were not always as pronounced (Fig. 4 c-f). These results indicate substantive qualitative and quantitative differences between the two frameworks, even when only one of the two functions is included.

Stability analysis indicated that: 1) interaction between prey-dependent death rate (Fig. 5a) and carrying capacity (*K*) resulted in altered states of population dynamics (Fig. 5c) and 2) no substantive changes in population dynamics occurred with interaction between prey-dependence of conversion efficiency (Fig. 5b) and carrying capacity (Fig. 5d).

Relatively small changes in the differences in conversion efficiency and death rate (Fig. 5a,b) between two consumers that were competing for the same resource revealed pronounced advantages for the superior competitor. This suggests that subtle differences in both these prey-dependent parameters will influence outcomes of competition, as illustrated by days to extinction of the inferior predator (Fig. 5e,f).

Discussion

Here we address "false exclusions" (*sensu* Topping 2015) by embedding aspects of predator performance into the classical structure for assessing predator-prey (consumer-resource) population dynamics. We show that prey-dependent performance associated with resource allocation (death rate, birth rate, and conversion efficiency) apply within and between lineages of zooplankton from marine and freshwaters, suggesting common phenomena (Fig. 1-3). Specifically, we delineate a conceptual framework (Fig. 2) and support it with empirical evidence (Fig. 3) to indicate that both the predator's conversion efficiency (*e*) and death rate (*d*) vary in a predictable manner with prey abundance. When embedded into the classical structure, these *e*- and *d*-responses result in marked changes (Fig. 4, 5). Consequently, we support their future consideration in bi-, tri-, and multi-trophic level models that are currently based on the classical structure (e.g., Carlotti *et al*. 2000; Lévy, 2015; de Ruiter and Gaedke 2017). Furthermore, as zooplankton are model organisms (e.g., Kooijman 2010), our findings will hopefully stimulate a wider audience to consider the revised resource-allocation structure (Eq. 5b) when assessing consumer-resource dynamics.

Considering the implications of this added complexity seems justified as we reveal qualitative and quantitative trends that differ from those predicted by the classical framework, trends that could affect predictions associated with trophic stability and ultimately ecosystem functioning. Furthermore, there is evidence, for a protozoan-based system, that embedding prey-dependent *per capita* growth rate (i.e., indirectly including prey-dependent *d* and *e*) in the classical structure improves a model's predictive ability, when compared to independent, experimentally obtained time-series data (Li and Montagnes 2015). Here, although we have not compared our predictions for zooplankton to independently obtained time-series data, we do find substantial differences between the two model structures, even when only one of the two prey-dependent functions is included (Fig. 4). Interestingly, the impact of prey-dependent *d* alone is greater in altering the bifurcation of the response and less in altering the pre-bifurcation response, while the impact of prey-dependent *e* alone is more similar, but not identical, to that of combining prey-dependent *e* and *d* (Fig. 4). This suggests interactions between these function should be explored in the future and that including both prey-dependent *e* and *d* may be needed to provide realistic predictions. Furthermore, both stability and competition analyses suggest that the impact of these responses on population dynamics may be profound and have wider implications (Fig. 5), with the competition analysis building on past arguments regarding resource competition (Tilman 1982). Our empirically-informed findings, therefore, provide strong evidence that: 1) where the classical structure is embedded in ecosystem models (specifically aquatic but also more generally) it may be prudent to add the complexity outlined by our resource allocation structure (Eq. 5b) and 2) theoretical studies that explore consumer-resource dynamics and competition-outcomes might at least carefully consider the influence of both prey-dependent conversion efficiency and death rates.

Why have prey-dependent e *and* d *not been fully appreciated?*

Arguably, resources are the most important driver of ecosystems. As such prey-dependent responses have long been integral to predator-prey and larger population models; e.g., logistic growth, the functional response, and occasionally the numerical response (Turchin 2003; Fenton *et al*. 2010; Arditi and Ginzburg 2012). Likewise, resource-dependent responses are employed to compare the functional biology of consumers (e.g., Tilman 1982) and have been directly or indirectly included in complex population models based on dynamic energy budgets (e.g., Nisbet *et al*. 2010). However, for the classical structure (Eq. 1, 2), prey-dependent death rate and conversion efficiency (Fig. 2) are rarely directly, or even indirectly, considered. Two recent exceptions are studies by Minter *et al*. (2011) and Montagnes and Fenton (2012); these indicated that when viewed in isolation prey-dependent death rate and conversion efficiency, respectively, both had substantive influence on predator-prey dynamics, relative to outcomes of the classical structure. However, to assess mortality, Minter *et al*. (2011) studied only one protozoan-based system and relied on published estimates for some parameters, and Montagnes and Fenton (2012) inappropriately used only published values of assimilation efficiency to predict conversion efficiency (values that were two-fold larger than those we have obtained), and their theoretical analysis of responses failed to recognise R_β and hence the decrease in e at low prey abundances.

Here we significantly build on the above works. We concurrently measured rates on individual species -with a focus on animals- (Fig. 3) and based the analysis on an improved theoretical evaluation (Fig. 2). In doing so, we indicate that both prey-dependent responses can independently alter predator-prey dynamics, and critically that their combined effect produces substantial differences in predator-prey dynamics compared to those produced by the classical structure (Fig. 4).

More generally, the influence of prey abundance on predator mortality and uptake efficiencies has been considered. Over three decades ago consumer death rate, especially at low resource levels, was recognised as critical in dictating competitive advantage (Tilman 1982). Likewise, there are indications that death rate will decrease with increasing prey abundance (Fig. 1). It, therefore, seems perplexing that, although Ginzburg (1998) alluded to this very issue, emphasis has not been placed on assessing or implementing prey-dependent mortality, with some notable exceptions (e.g., Carlorri *et al*. 2002; Tian 2006; Minter *et al*. 2011) and with a recognition that prey-dependent mortality can be accounted for in the more complex dynamic energy budget models (e.g., Nisbet *et al*. 2010). Similarly, four decades ago, Calow (1977) reviewed the literature on assimilation efficiency ($\varepsilon = [I\text{-}E]/I$, where I is ingestion and E is egestion), some of which was already over 30 years old, and remarked on its prey-dependence. Likewise, Straile (1997) remarked on the prey-dependency of gross growth efficiency (GGE = r/I). Since then there have been numerous examples of prey-dependent ε and GGE (e.g., Fig. 1; Giguère 1981; Kremer and Reeve 1989; Urabe and Watanabe 1991; Jumars 2000; Kimmance *et al*. 2006; Lombard *et al*. 2009; Kooijman 2010) but little attention to the prey-dependency of conversion efficiency (*e*). Both ε and GGE may be incorporated into predator-prey models, as surrogates of *e*, but they are not *e*, which is central to the classical predator-prey structure (Eq. 2, 3b, 5a). Furthermore, except for a handful of analyses regarding how prey-dependent "efficiency" might affect predator-prey dynamics and predator growth (Franks *et al*. 1986; Mitra and Flynn 2007; Flynn 2009; Fenton *et al*. 2010; Montagnes and Fenton 2012), there has been little exploration of such prey-dependent "energetic efficiencies" on population dynamics using the classical structure.

There are several explanations for the current neglect of *e* and *d* prey-dependence. First, parsimony of the standard predator structure (Eq. 2, 3b, 5a), where *e* and d_0 are invariant, makes it appealing, a view reflected by the ecological canon (e.g., Peters 1983; Turchin 2003; Arditi and Ginzburg 2012; Begon *et al*. 2012). Also, only requiring d_0 and I_τ (as outlined above, *A revision of the classical predator-prey model,* Eq. 3b) has undoubtedly played a role, as these can be relatively simple to measure; in contrast, obtaining multiple rates, especially at low abundances is challenging.

Still, for ~100 years ecologists have improved on the current classical framework (as outlined by Turchin 2003; Arditi and Ginzburg 2012), adding complexity where needed. In that tradition, we show that when attention is paid to obtaining and applying measurements of prey-dependent *e* and *d* (Fig. 2, 3, Table 1), marked differences in the predictions of predator-prey dynamics occur (Fig. 4, 5). This provides compelling evidence that specifically plankton biologists, and recognising zooplankton as model organisms all ecologists, should consider parameterizing these predator responses.

Assessing prey-dependent responses also provides insights into organismal performance. For instance, consider assimilation efficiency (ε): if the energy needed for survival and reproduction (I_τ, Fig. 2) is a large component of the energy ingested (I), then conversion efficiency, $e = (I\text{-}E\text{-}\ I_\tau)/I$, will be significantly lower than ε at sub-saturating prey abundances, as appears to be so (Fig. 1, 3). Likewise, at low prey levels as $R \rightarrow R_\beta$, then $e \rightarrow 0$ (Fig. 2), but measurements at low prey abundance are rare and require attention, as this is where responses may vary most (Fig. 1-3), potentially conferring competitive advantages (Fig. 5f, Hassell *et al*. 1977; Tilman 1982). Understanding why responses change at low prey abundances may also provide mechanistic insights, akin to the behavioural shifts reflected by Type III functional responses (Hassell *et al*. 1977; Real 1977; Jeschke *et al*. 2002; Turchin 2003). For instance, I_β (Fig. 2) might represent the energy required to: maintain structures for egg production; find and interact with mates; or reach and maintain a critical size before investing energy towards reproduction. Such costs have been considered in the context of understanding dynamic energy budgets (Lika and Kooijman 2003, Kooijman 2010) and evolutionary and behavioural trade-offs between the allocation to somatic growth and reproduction (Reznick *et al*. 2000; Sarma *et al*. 2002; Speakman 2008). As a cautionary note, we emphasise that measurements at low prey abundances are subject to high variability due to experimental error and stochasticity associated with measuring few prey. Estimates of R_β by our methods, which rely on predicting growth and death rates at low prey abundances, must then be obtained from multiple treatments at low abundances, as we have done.

How might we progress?

Our revised resource allocation structure (Eq. 5b) offers opportunities for exploring trophic stability, ecosystem dynamics, and functional biology. For instance, both abiotic (e.g., temperature) and biotic (prey quality and size) factors affect energetic efficiencies and death rates (e.g., *Chlorella* sp. vs *Phaeocystis globosa* as food for *Brachionus plicatilis* in Fig. 3; McConnachie and Alexander 2004; Kimmance *et al*. 2006; Mitra and Flynn 2007; Yang *et al*. 2013). Likewise, following arguments of Arditi and Ginzburg (2012) it may be that both *e* and *d* also depend on predator abundance (Brown *et al*. 1994; Ohman and Hirche 2001; Forrester and Steele 2004), providing a framework for the further investigation of ratio dependent responses. Equally possible is that *e* and *d* may vary with nutritional history (i.e., past prey abundances in a fluctuating environment), as both the functional and numerical responses are altered by past prey levels (Li *et al*. 2013; Li *et al*. 2018). Finally, if the functional and numerical responses are better predicted by sigmoidal (i.e., Type III responses) rather than the rectangular hyperbolic functions that we assumed (i.e., Type II), shifts in rates at low prey abundances may alter predictions of *e* at these low abundances. Future efforts might explore these added complications in the context of our revised structure.

There are empirical and computational methods for providing prey dependent estimates of *e* and *d*, but the experimental challenges we face depend on the system and the animals. For instance, standard techniques can determine assimilation efficiency (ε) for large animals, by measuring the biomass (or caloric content) of ingested and egested materials (Calow1977; Southwood1978; Båmstedt *et al*. 2000; Henderson 2016), although for some large animals (e.g., in aquatic systems) collecting faeces may be impossible, and using isotopes-tracers is a more pragmatic approach (Båmstedt *et al*. 2000). Likewise, for large animals, methods exist to determine maintenance and reproductive costs (Sarma 2002; Speakman 2008; Henderson 2016). It may then be possible, following logic laid out in the Introduction, to predict prey-dependent conversion efficiency (*e*) for many large animals. In contrast, death rate measurements for larger, long-lived animals may be challenging (Krebs, 1989), either in nature or under controlled conditions, and often proxies or indices must be relied upon (e.g., Fig. 1j); new methods to estimate prey-dependent death rate are needed. For small organisms, (e.g., insects, nematodes, zooplankton, meiofauna), with relatively rapid rates, death rate may be assessed by the methods we provide here (Fig. 3; Minter *et al*. 2011), but determining ε, where egested material is minute, is problematic. Furthermore, determining and separating metabolic costs associated with maintenance and reproduction may be challenging for small animals (Runge and Roff 2000). However, for small animals, directly measuring *per capita* growth rates is relatively simple, and we have shown here how these may be used to assess e. Finally, in the Introduction (Fig. 2) we highlight that if the ratio of prey needed for producing new individuals is large relative to that for survival (e.g., $R_\beta : R_\tau > 1$), then the numerical response is not smooth (Fig. 2d, large-dashed line); for animals that invest substantial energy into reproduction a more complex analysis may be necessary to assess conversion efficiencies. In summary, applying multiple approaches is undoubtedly the solution to appreciate the magnitude of prey-dependent conversion efficiency and death rate, so that these vital rates may be incorporated into future models across all taxa.

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Appendix 1 Experimental details

Table A1 Details of the design for the functional, numerical, and mortality response experiments. *At low prey abundances, where growth rate was negative and thus numbers decreased, initial numbers were higher, up to 80 individuals in some cases; this was to allow accurate estimates of decline over more than one day.

Predator	Prey	Response	Predator number	Container volume (ml)	Duration	Temperature (°C)
Brachionus calyciflorus	Chlorella sp. (freshwater)	functional	50 (n=1)	10	20-120 min	21
		numerical	*10 (n=1)	10	4-5 days	
		mortality	1 (n=50)	3	5-6 days	
Brachionus plicatilis	*Chlorella sp.* (marine)	functional	1000 (n=1)	30	20-120 (min)	25
		numerical	*10 (n=1)	10	4-5 days	
		mortality	1 (n=50)	3	5-6 days	
Brachionus plicatilis	*Phaeocystis globosa*	functional	1000 (n=1)	30	20-120 (min)	25
		numerical	*10 (n=1)	10	4-5 days	
		mortality	1 (n=50)	3	5-6 days	
Daphnia magna	*Chlorella* sp. (freshwater)	functional	100	50	20-120 (min)	25
		numerical	*50	1000	4-5 days	
		mortality	1 (n=50)	10	5-6 days	
Moina macrocopa	*Chlorella* sp. (freshwater)	functional	100	50	20-120 (min)	25
		numerical	*50	1000	4-5 days	
		mortality	1 (n=50)	10	5-6 days	
Didinium nasutum	*Paramecium caudatum*	functional	100	10	5-30 (min)	25
		numerical	*2	10	4-5 days	
		mortality	1 (n=50)	3	5-6 days	

Appendix 2, An assessment of fitting Type II and Type III responses to the functional and numerical response data

We examined the goodness of fits for rectangular hyperbolic (Type II) and sigmoidal (Type III) functional and numerical responses to data presented in Fig. 3 (main text). For the functional response we fit functions of the form $I = I_{max}*R/(k+R)$, or $I = I_{max}*R^2/(k^2+R^2)$. For the numerical response, we fit functions of the form $r = r_{max} *(R- R_\tau)/(k_2+R- R_\tau)$ or $r = r_{max} *(R^2- R_\tau^2)/(k_2^2+R^2- R_\tau^2)$. All parameters and variables are described in the main text. Goodness of fit was assessed for all consumers by examining *AIC*c and adjusted R^2 values, with lower *AIC*c and higher adjusted R^2 values representing a better fit.

For some of the fits to responses there is a slight improvement by applying a sigmoidal function, but for others it is worse. Critically the differences are relatively small (Table A2). We suggest that given the variability of the data, it is possible that a random shift of a few points at the lower end of the prey abundances may have pushed the response to appear more (or less) sigmoidal. Statistical analysis to support either function would require substantially more data in this lower region, which was not the emphasis of our work. Furthermore, for the one response that does appear slightly sigmoidal (that of *Didinium nasutum* feeding on *Paramecium caudatum*) other reports (e.g. Li and Montagnes 2015, which used the same methods we have used and we have cited in the main text) have not seen a sigmoidal response. We concluded that it seems prudent to evaluate the issues we are addressing by assuming a rectangular hyperbolic function, which does seem to adequately represent the data. However, we recognise that a Type III response in either or both the functional or numerical responses would alter the shape to the response of conversion efficiency to prey abundance. This may be worth pursuing in the future.

Table A2 *AIC*c and adjusted R^2 values for fits to Type II and III functional and numenrical responses. Fits are provided for the consumers: *Brachionus calciflouris* (BC), *B. plicatilis* fed *Cholrella vulgaris* (BPC), *B. plicatilis* fed *Phaeocystis globosa* (BPP), *Monia macrocopa* (MM), *Daphnia magna* (DM),and *Didinium nasutum* (DN).

Response	Type	Metric	BC	BPC	BPP	MM	DM	DN
Functional	Type II	AICc	46.00	81.13	88.85	279.06	171.13	15.46
Functional	Type III	AICc	49.08	88.29	102.64	289.03	168.45	11.13
Numerical	Type II	AICc	-59.42	-56.71	-34.52	-72.23	-63.64	-54.26
Numerical	Type III	AICc	-60.67	-65.72	-36.02	-57.36	-63.61	-62.30
Functional	Type II	Adjusted R^2	0.801	0.985	0.960	0.973	0.946	0.881
Functional	Type III	Adjusted R^2	0.765	0.977	0.904	0.956	0.955	0.905
Numerical	Type II	Adjusted R^2	0.876	0.939	0.807	0.961	0.828	0.899
Numerical	Type III	Adjusted R^2	0.884	0.963	0.827	0.911	0.828	0.927

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Table 1 Abundance-based parameters for predator-responses and estimates of predator and prey biomass. Parameters values are presented with their respective standard errors (directly below) for the functional (Eq. 4b), numerical (Eq. 6), and mortality (Eq. 7) responses. Estimates of R_β were obtained from (Fig. 3). Parameters for the "Generic Predator" were used in model simulations (see Methods). Biomass was determined as carbon content (Elementar Analysensysteme GmbH, Germany), unless otherwise stated: *biomass obtained from Pauli (1989); **biomass obtained from Rocha and Duncan (1985); *** biovolumes were determined from ~50 randomly chosen cells, and biovolume was assumed a good estimate of biomass.

Predator (biomass) **Prey (biomass)**	I_{MAX} R min^{-1}	k R ml^{-1}	r_{MAX} d^{-1}	k_2 R ml^{-1}	$R\tau$ R ml^{-1}	R_β R ml^{-1}	d_{MIN} R ml^{-1}	α mlR^{-1}d^{-1}	k_δ R ml^{-1}
Brachionus calyciflorus (150 ng)*	78.8	337600	0.521	237700	136500	112000	0.061	0.371	1050
Chlorella vulgaris (5 pg)**	(6.7)	(108000)	(0.14)	(65400)	(29600)		(0.012)	(0. 031)	(534)
Brachionus plicatilis (130 ng)	288	1410000	0.928	1298000	647700	45500	0	0.857	680800
Chlorella sp. (marine) (9.6 pg)	(19)	(155800)	(0.067)	(299200)	(115600)			(0.076)	(258500)
Brachionus plicatilis (130 ng)	223	1654000	0.424	763300	460200	1000	0.0006	0.645	399700
Phaeocystis globosa (12 pg)	(16.0)	(323000)	(0.120)	(423300)	(223400)		(0.070)	(0.110)	(275600)
Moina macrocopa (3360 ng)	173250	750600	0.968	95970	24000	9200	0.0529	0.358	4960
Chlorella sp. (fresh water) (2 pg)	(800)	(115000)	(0.043)	(24700)	(5400)		(0.0186)	(0.0412)	(3780)
Daphnia magna (9304.6 ng)	3390	194600	0.390	119200	62700	17000	0	0.324	52400
Chlorella sp. (fresh water) (2 pg)	(230)	(37900)	(0.06)	(35200)	(14300)			(0.034)	(13300)
Didinium nasutum (3.0 x 10^5 μm^3)***	0.0123	91.09	2.079	36.62	9.690	2.4	0	0.588	18.71
Paramecium caudatum (3.2 x 10^5 μm^3)***	(0.00165)	(25.65)	(0.232)	(9.256)	(1.550)			(0.0547)	(4.84)
Generic Predator (10000 ng)	70	2000000	0.7	800000	600000	150000	0.1	2	100000
Generic Prey (1 ng)									

Figure Legends

Fig. 1 Examples of how conversion (e) and assimilation efficiencies (i.e., [ingestion – egestion]/ingestion) (a-e) and death (d) rates (f-j) vary with prey abundance. Data points are from the literature, and lines (b-j) illustrate trends. a. Predictions of conversion efficiency of the ciliate *Didinium* grown on the ciliate *Paramecium* (Li and Montagnes 2015). b. Assimilation efficiency for the copepod *Acartia tonsa* feeding on the diatom *Thalassiosira weissflogii* (Besiktepe and Dam 2002). c. Assimilation efficiency for the larvacean *Oikopleura dioica*, fed *Thalassiosira pseudonana* (Lombard *et al*. 2009). d. Assimilation efficiency for the brine shrimp *Artemia franciscana*, fed the alga *Isochrysis galbana* (Evjemo *et al*. 2000). e. Assimilation efficiency for the sea urchin *Strongylocentrotus droebachiensis*, fed a mixture of kelp and mussel tissue (Thompson 1982). f. *per capita* death rate of *Didinium* grown on *Paramecium* (Minter *et al*. 2011). g. *per capita* death rate of larval striped bass, *Morone saxatilis*, feeding on brine shrimp, *Artemia salaina*, nauplii (Eldridge *et al*. 1981). h. *per capita* death rate of the water flea *Daphnia pulex*, feeding on the alga *Chlamydomonas reinhardtii* (Paloheimo and Taylor 1987). i. death rate (% of population) of South American sea lion pups, *Otaria flavescens*, in relation to available food, fish, *Enagraulis ringes* (Soto *et al*. 2004). j. mortality index of killer whales, *Orcinus orca*, in relation to an index of one food source, fish, *Oncorhynchus tshawytscha* (Ford *et al.* 2010).

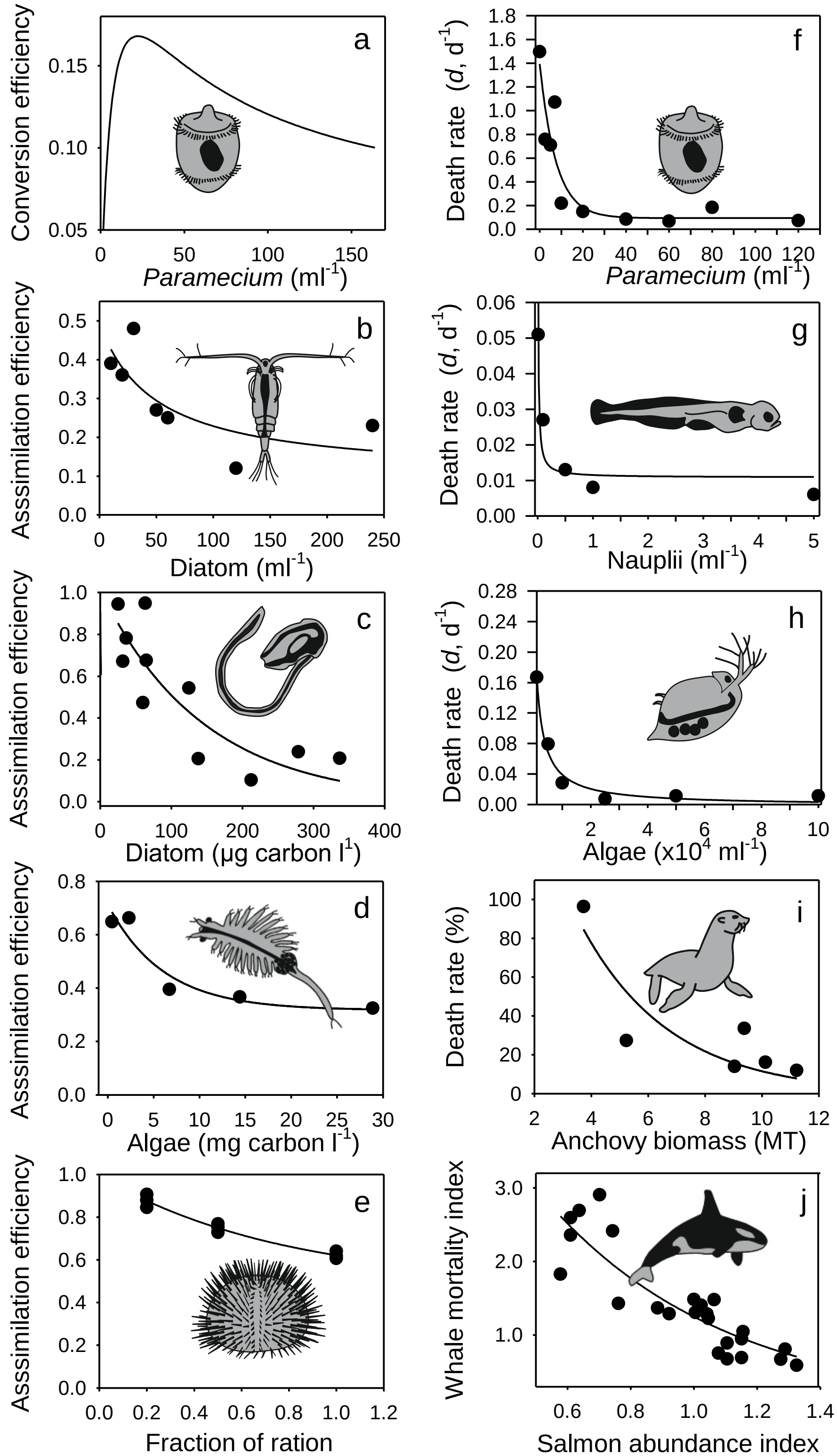
Fig. 2 Simulations of predator responses to change in prey abundance: (a) ingestion, I; (b) births, b; (c) deaths, d; (d) specific growth rate, r, and (e) conversion efficiency, e. Equations for response are presented in the panels, with: R = prey abundance (range 0 to 75); $I_{\mathrm{MAX}} = 20$; $k = 30$; $b_{\mathrm{MAX}} = 20$; $k_{\beta} = 10$ $R_{\beta} = 0$ (short dashed lines), 2 (solid lines), and 15 (long dashed lines); $\alpha = 10$; $k_{\delta} = 3$; $d_{\mathrm{MIN}} = 1$; R_{β} is the prey abundance required to provide I_{β} (i.e., below which births do not occur). R_{τ} is the prey abundance where $b - d = 0$. Note, all values were chosen for illustration purposes and do not represent a specific biological system, and therefore scales are not included on this figure.

Fig. 3 Responses of the model predators (*Brachionus calyciflorus, B. plicatilis, Moina macrocopa, Daphnia magna, Didinium nasutum*) and the "Generic predator" (used in the model simulations) to change in prey abundance (*Chlorella vulgaris, Chlorella* sp. [both marine and freshwater species], *Phaeocystis globose, Paramecium caudatum*; see Table 1 for details). Presented are the functional response (Eq. 4b, row 1); numerical response (Eq. 6, row 2); mortality response (Eq. 7, row 3); birth rate response (row 4); and conversion efficiency response (row 5). Responses (lines) were fit to data (for the parameters of the responses see Table 1). Solid lines are the fit through the data. Dashed lines are the 95% confidence boundaries for the response. Adjusted R^2 values for the fits of curves to data are presented on individual panels. The birth rate and conversion efficiency responses were determined from the functional, numerical, and mortality responses (see Materials and Methods, Table 1). The Generic predator responses were generated from parameters presented in Table 1. *The scale for ingestion (I) rate of *D. nasutum* (XXVI) is in units of prey per hour. Note that the x-axis for all *M. macrocopa* responses have an origin of -10^4 to reveal the trend in panel xx.

Fig. 4 Bifurcation diagram showing, the effect of increasing prey carrying capacity (K) on survival, extinctions, and the maxima and minima of the limit cycle, of the generic prey (a, c, e) and generic predator (b, d, f) in the classical model described by Eq. 4a and 5a (dashed line) and the revised resource allocation model structure described by Eq. 4a and 5b (solid line). See Methods for a description of the how the combined and independent effects of variable e and d were applied to the model structure (c-f). Model parameters are described in the text and Table 1 as generic predator and prey.

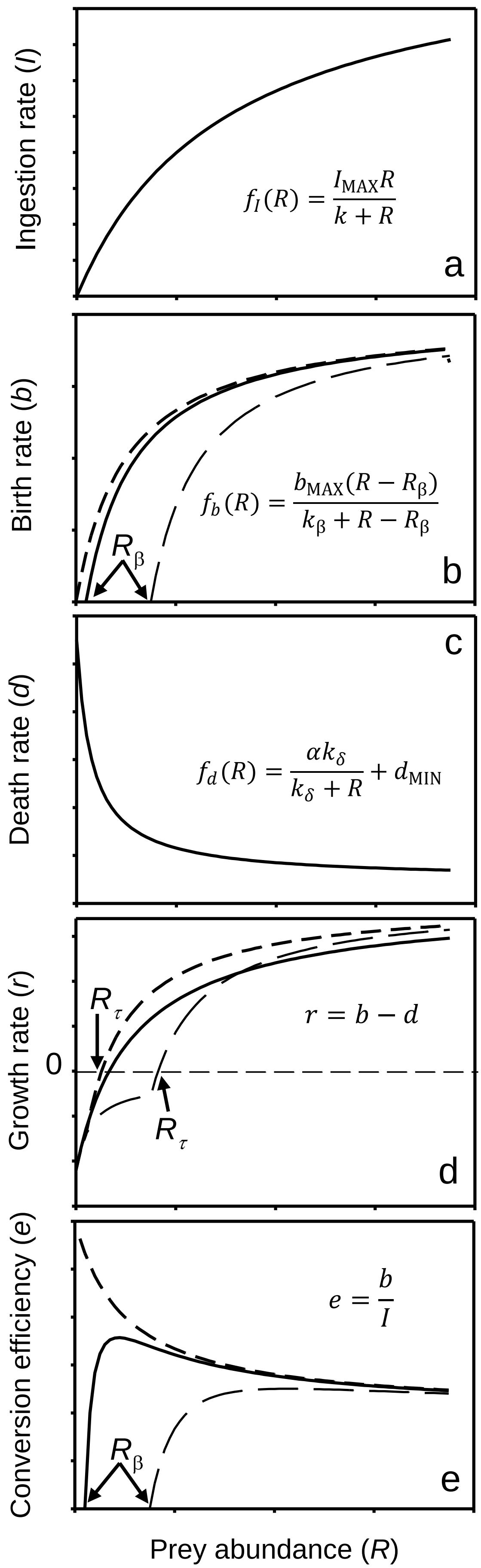
Fig. 5 Comparisons of varying prey-dependent predator mortality and conversion efficiency responses. (a, b) the range of variation of the mortality and conversion efficiency responses, based on the generic predator parameters (Table 1) and attributes displayed by experimental animals (Fig. 3); these were then applied to the resource allocation predator-prey model (see Materials and Methods and Eq. 4a, 5b). Stability boundary analysis for the resource allocation model under (c) different mortality responses and (d) different conversion efficiency responses, as described in (a) and (b). (e, f) days to extinction of the inferior competitor (C_2), following the resource allocation model described by Eq. 9,10; note, initial numbers of both predators were 1 ml^{-1}, with extinction operationally defined as 10^{-2} predators ml^{-1}.

Figure



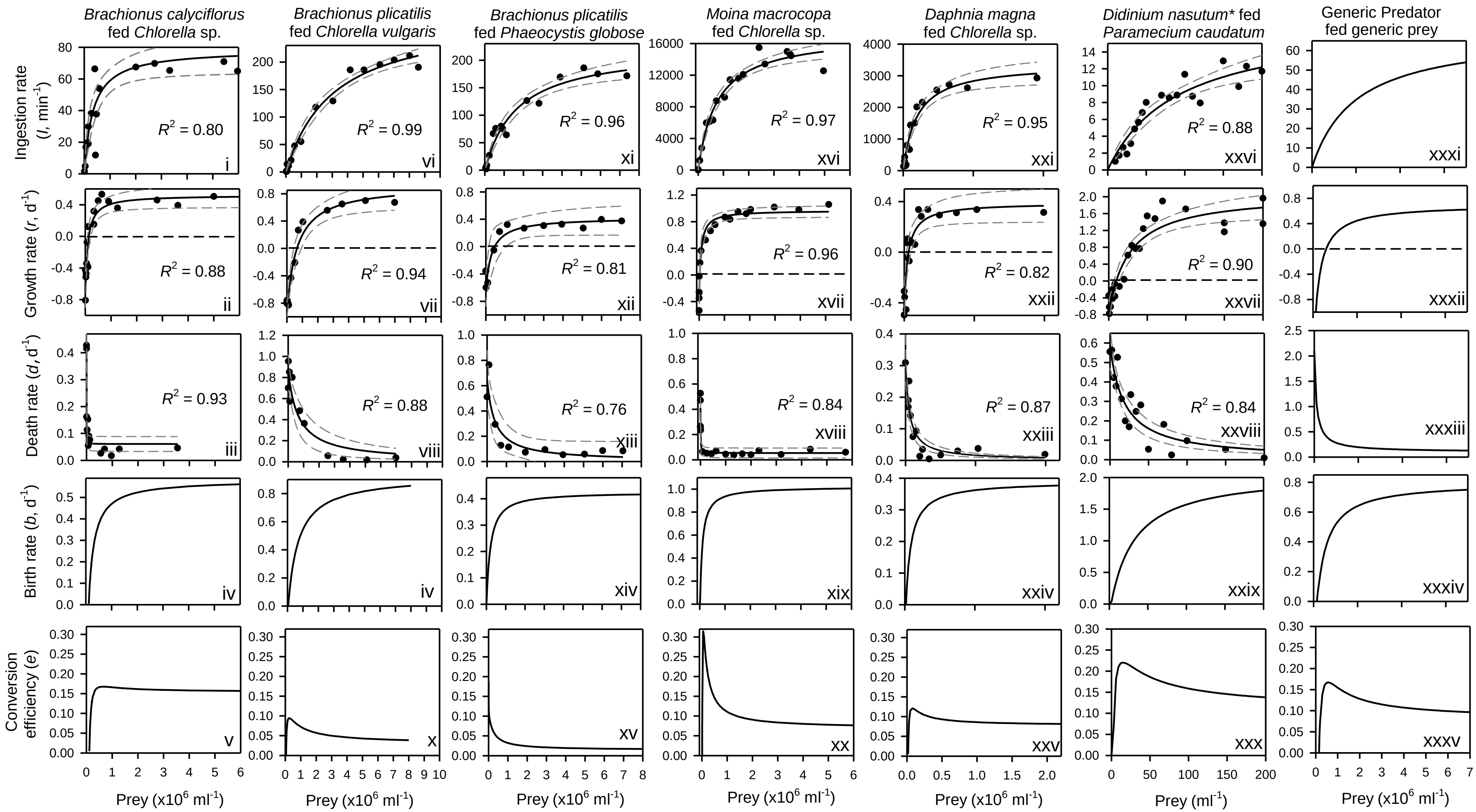
a
Conversion efficiency
0.05
0.10
0.15
0
50
100
150
Paramecium (ml-1)
f
Death rate (d, d-1)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
0
20
40
60
80
100
120
Paramecium (ml-1)
b
Asssimilation efficiency
0.0
0.1
0.2
0.3
0.4
0.5
0
50
100
150
200
250
Diatom (ml-1)
g
Death rate (d, d-1)
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0
1
2
3
4
5
Nauplii (ml-1)
c
Asssimilation efficiency
0.0
0.2
0.4
0.6
0.8
1.0
0
100
200
300
400
Diatom (μg carbon l-1)
h
Death rate (d, d-1)
0.00
0.04
0.08
0.12
0.16
0.20
0.24
0.28
2
4
6
8
10
Algae (x10^4 ml-1)
d
Asssimilation efficiency
0.0
0.2
0.4
0.6
0.8
0
5
10
15
20
25
30
Algae (mg carbon l-1)
i
Death rate (%)
0
20
40
60
80
100
2
4
6
8
10
12
Anchovy biomass (MT)
e
Asssimilation efficiency
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Fraction of ration
j
Whale mortality index
1.0
2.0
3.0
0.6
0.8
1.0
1.2
1.4
Salmon abundance index

Figure



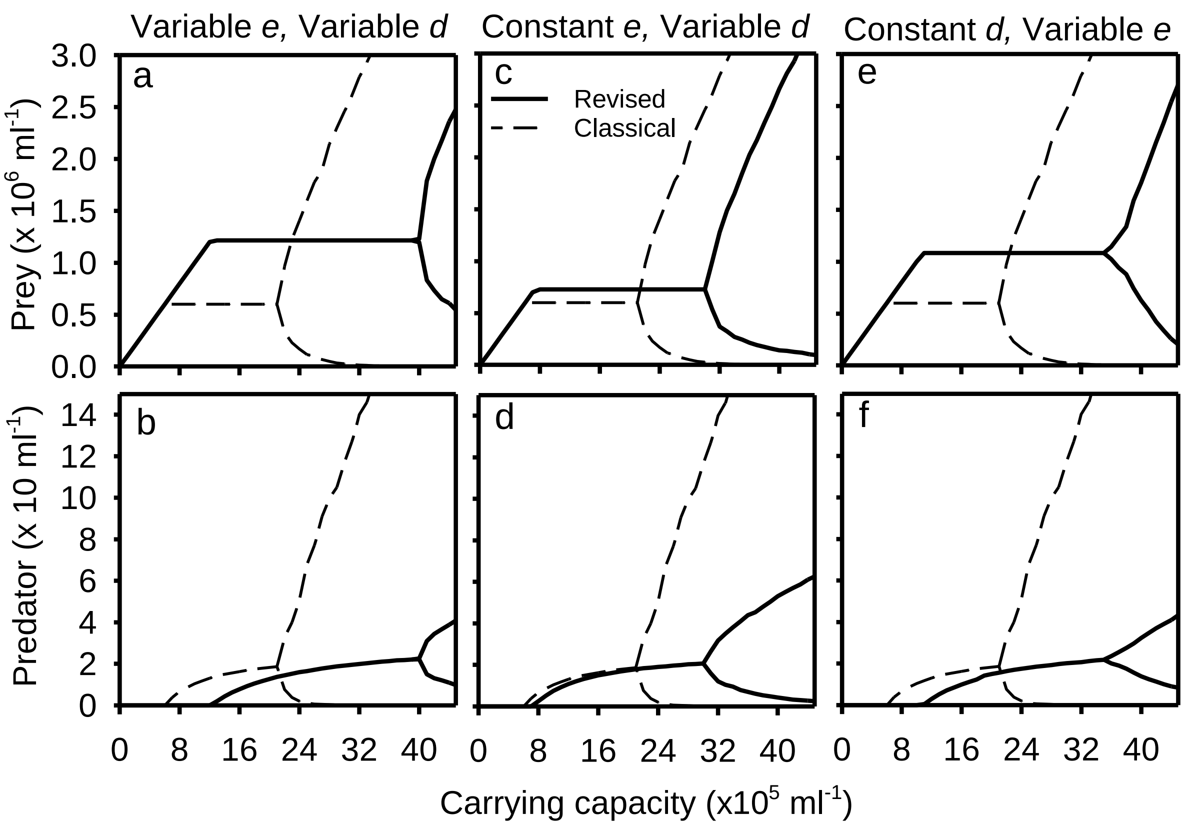
Ingestion rate (I)
$f_I(R) = \frac{I_{\mathrm{MAX}}R}{k + R}$
a
Birth rate (b)
$f_b(R) = \frac{b_{\mathrm{MAX}}(R - R_\beta)}{k_\beta + R - R_\beta}$
R_β
b
Death rate (d)
$f_d(R) = \frac{\alpha k_\delta}{k_\delta + R} + d_{\mathrm{MIN}}$
c
Growth rate (r)
$r = b - d$
0
R_τ
R_τ
d
Conversion efficiency (e)
$e = \frac{b}{I}$
R_β
e
Prey abundance (R)

Figure



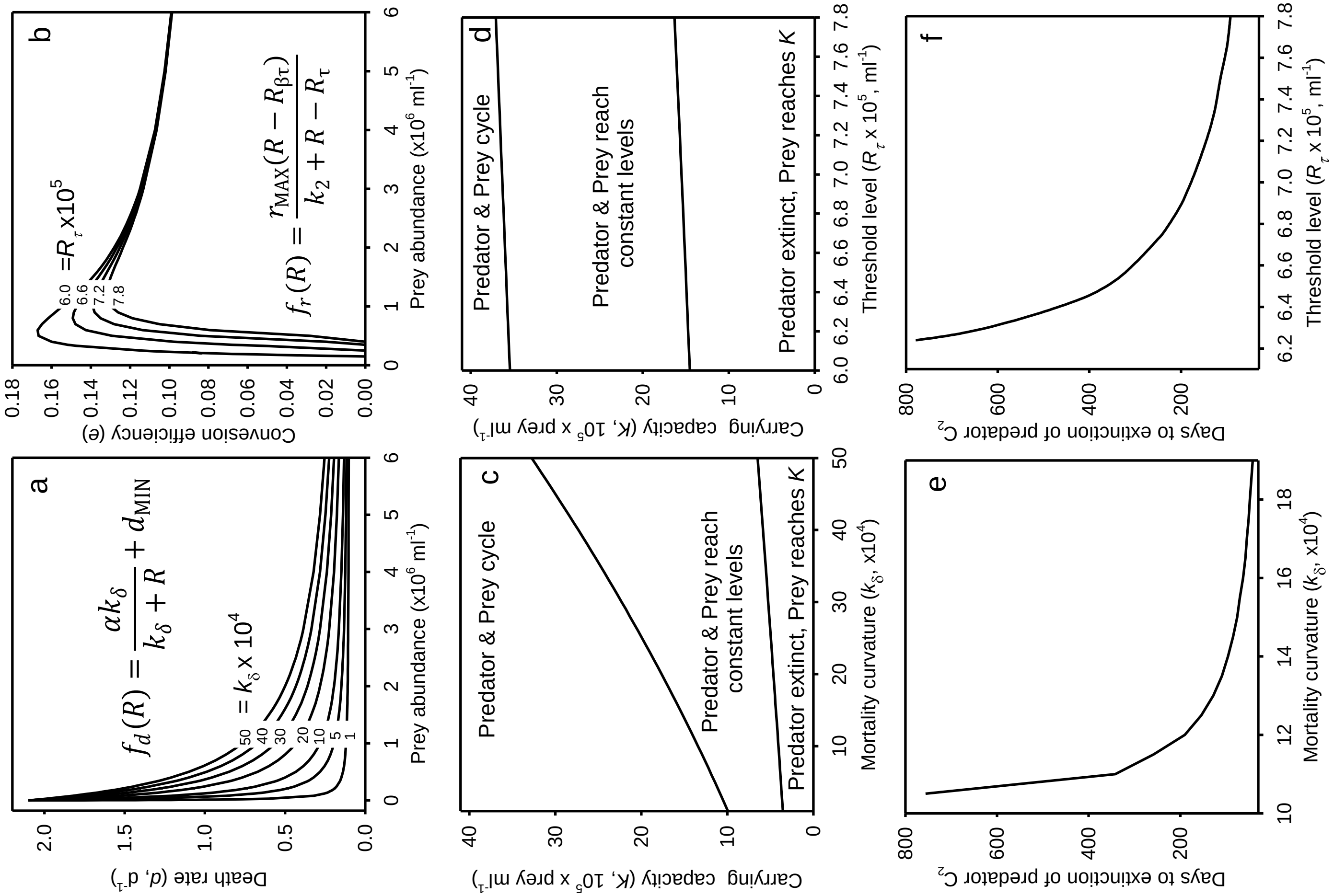
Brachionus calyciflorus fed Chlorella sp.
Brachionus plicatilis fed Chlorella vulgaris
Brachionus plicatilis fed Phaeocystis globose
Moina macrocopa fed Chlorella sp.
Daphnia magna fed Chlorella sp.
Didinium nasutum* fed Paramecium caudatum
Generic Predator fed generic prey
Ingestion rate (I, min-1)
Growth rate (r, d-1)
Death rate (d, d-1)
Birth rate (b, d-1)
Conversion efficiency (e)
Prey (x10^6 ml-1)
Prey (ml-1)
R2 = 0.80
R2 = 0.99
R2 = 0.96
R2 = 0.97
R2 = 0.95
R2 = 0.88
R2 = 0.88
R2 = 0.94
R2 = 0.81
R2 = 0.96
R2 = 0.82
R2 = 0.90
R2 = 0.93
R2 = 0.88
R2 = 0.76
R2 = 0.84
R2 = 0.87
R2 = 0.84
i
ii
iii
iv
v
vi
vii
viii
iv
x
xi
xii
xiii
xiv
xv
xvi
xvii
xviii
xix
xx
xxi
xxii
xxiii
xxiv
xxv
xxvi
xxvii
xxviii
xxix
xxx
xxxi
xxxii
xxxiii
xxxiv
xxxv

Figure



Variable e, Variable d
Constant e, Variable d
Constant d, Variable e
a
b
c
d
e
f
Revised
Classical
Prey (x 10^6 ml^-1)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Predator (x 10 ml^-1)
14
12
10
8
6
4
2
0
0
8
16
24
32
40
Carrying capacity (x10^5 ml^-1)

Figure



a
$f_d(R) = \frac{\alpha k_\delta}{k_\delta + R} + d_{MIN}$
$= k_\delta \times 10^4$
50
40
30
20
10
5
1
Death rate (d, d^{-1})
Prey abundance ($\times 10^6$ ml^{-1})
b
$=R_\tau \times 10^5$
6.0
6.6
7.2
7.8
$f_r(R) = \frac{r_{MAX}(R - R_{\beta\tau})}{k_2 + R - R_\tau}$
Conversion efficiency (e)
Prey abundance ($\times 10^6$ ml^{-1})
c
Predator & Prey cycle
Predator & Prey reach constant levels
Predator extinct, Prey reaches K
Carrying capacity (K, 10^5 x prey ml^{-1})
Mortality curvature (k_δ, $\times 10^4$)
d
Predator & Prey cycle
Predator & Prey reach constant levels
Predator extinct, Prey reaches K
Carrying capacity (K, 10^5 x prey ml^{-1})
Threshold level (R_τ x 10^5, ml^{-1})
e
Days to extinction of predator C_2
Mortality curvature (k_δ, $\times 10^4$)
f
Days to extinction of predator C_2
Threshold level (R_τ x 10^5, ml^{-1})

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