

Transient dynamics and the destabilizing effects of prey heterogeneity

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Abstract. The presence of prey heterogeneity and weakly interacting prey species is frequently viewed as a stabilizer of predator–prey dynamics, countering the destabilizing effects of enrichment and reducing the amplitude of population cycles. However, prior model explorations have largely focused on long-term, dynamic attractors rather than transient dynamics. Recent theoretical work shows that the presence of prey that are defended from predation can have strongly divergent effects on dynamics depending on time scale: prey heterogeneity can counteract the destabilizing effects of enrichment on predator–prey dynamics at long time scales but strongly destabilize systems during transient phases by creating long periods of low predator/prey abundance and increasing extinction probability (an effect that is amplified with increasing enrichment). We tested these general predictions using a planktonic system composed of a zooplankton predator and multiple algal prey. We first parameterized a model of our system to generate predictions and tested these experimentally. Our results qualitatively supported several model predictions. During transient phases, presence of defended algal prey increased predator extinctions at low and high enrichment levels compared to systems with only a single edible prey. This destabilizing effect was moderated at higher dilution rates, as predicted by our model. When examining dynamics beyond initial oscillations, presence of the defended prey increased predator–prey temporal variability at high nutrient enrichment but had no effect at low nutrient levels. Our results highlight the importance of considering transient dynamics when assessing the role of stabilizing factors on the dynamics of food webs.

Key words: *Ankistrodesmus falcatus*; *Brachionus calyciflorus*; *Cosmarium spp.*; *paradox of enrichment*; *predator–prey model*; *prey heterogeneity*; *rotifer–algal food web*; *stability*; *transient dynamics*; *weak interactions*.

INTRODUCTION

The presence of heterogeneity among species in the strength of their trophic interactions is commonly thought to exert a stabilizing influence on the dynamics of model food webs (May 1973, Pimm 1982, Kretzschmar et al. 1993, Abrams and Walters 1996, McCann et al. 1998). In his well-known explorations of community stability, May (1973) showed that reducing the average strength of species interactions could counter the destabilizing influence of complexity and species richness by increasing the probability that food webs would be resilient. Thus, the presence of species that interact weakly with other species can counter the destabilizing effects of strong trophic interactions. More recent investigations have expanded on this theme by considering a greater diversity of dynamic phenomena such as limit cycles and chaos (Kretzschmar et al. 1993, Abrams

and Walters 1996, McCann et al. 1998, Genkai-Kato and Yamamura 1999). These studies consolidate the view that weak interactions can exert strong stabilizing effects on consumer–resource interactions, moving systems to stable attractors or reducing the amplitude of population cycles. While such studies have been valuable, many natural systems experience periodic disturbances and environmental variation on timescales shorter than those required to reach the dynamic attractors considered in these studies. Hence, the dynamics of many communities may be better described as transient in nature (DeAngelis and Waterhouse 1987, Hastings 2001, 2004). Theoretical studies have begun to appreciate the importance of examining ecological dynamics when systems are far from their dynamic attractors (e.g., Neubert et al. 2004, Noonburg and Abrams 2005, Jäger et al. 2008, Steiner et al. 2009, Klausmeier 2010). These studies have revealed that dynamic outcomes during transient phases may diverge greatly from predictions at long time scales (Neubert and Caswell 1997, Neubert et al. 2004, Noonburg and Abrams 2005).

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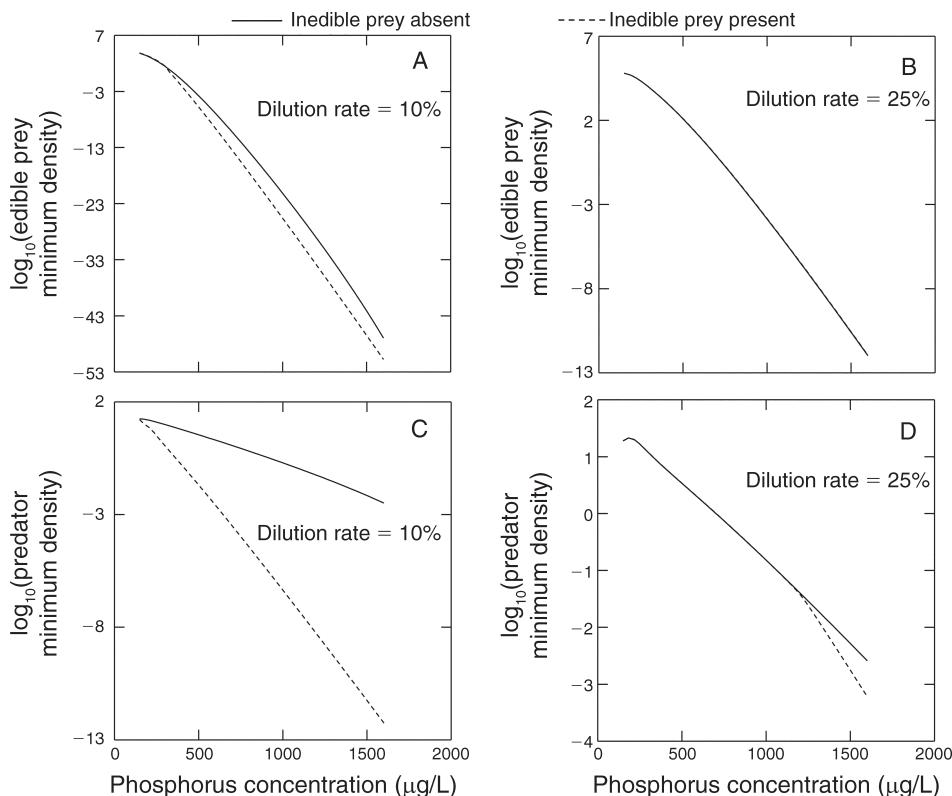


FIG. 1. Model predictions of the effects of enrichment, weak trophic interactions (inedible-prey presence/absence), and dilution rate on transient dynamics of the predator and the edible prey. Shown are effects on minimum densities (inversely related to extinction probability) following the first transient oscillation of (A) the edible prey at a 10% per day dilution rate, (B) the edible prey at a 25% per day dilution rate, (C) the predator at a 10% per day dilution rate, and (D) the predator at a 25% per day dilution rate. Lines are cubic spline fits through model data points. Density was originally measured as number/mL.

An ecological context in which the importance of weak interactions has been explored extensively is the effect of enrichment on predator-prey dynamics (Kretzschmar et al. 1993, Grover 1995, Abrams and Walters 1996, Bohannan and Lenski 1997, McCauley et al. 1999). Enrichment is known to exert a strong destabilizing influence on the long-term dynamics of simple predator-prey models that incorporate nonlinear functional responses. As the carrying capacity of prey increases in such models, predator-prey dynamics can move from stable point equilibria to limit cycles of increasing amplitude, enhancing the probability of predator or prey extinction (Rosenzweig 1971, May 1972, Gilpin 1972). Termed the “paradox of enrichment” by Rosenzweig (1971), this prediction is perhaps most notable for its apparent rarity in natural or experimental communities; while predator-prey systems can exhibit oscillatory dynamics in nature, few are known to exhibit a concomitant increase in cycle amplitude or extinction probability with increasing system enrichment (McCauley and Murdoch 1990, Kirk 1998, Persson et al. 2001, Turchin 2003, Jensen and Ginzburg 2005, Steiner et al. 2005, although see Luckinbill 1973, Veilleux 1979, Fussmann et al. 2000). As an explanation, models, as well as a handful of

experimental studies, have shown that the presence of prey heterogeneity and weakly interacting prey species can reduce population-level temporal variability and potentially temper the paradox of enrichment (Kretzschmar et al. 1993, Grover 1995, McCann et al. 1998, McCauley et al. 1999, Persson et al. 2001, Jiang et al. 2009). In these models, prey species are often assumed to trade-off competitive ability with the ability to avoid predation. Thus, the weakly interacting prey is a poor resource competitor (interacting weakly with its resource) but is more resistant to predation (interacting weakly or not at all with the top consumer) (see McCann et al. 1998: Fig. 1B, C). With this trade-off structure, predators can facilitate the invasion of the predator-resistant prey, which then acts as a nutrient sink, reducing the effective carrying capacity of the predator and edible prey. This can shift predator-prey cycles to stable point equilibria in some cases or reduce the amplitude of limit cycles depending on model parameters and level of enrichment (Kretzschmar et al. 1993, Grover 1995, McCann et al. 1998, McCauley et al. 1999). Similar effects can emerge when the predator-resistant prey interferes with predator feeding (Kretzschmar et al. 1993). In either case, variability and the

probability of extinction of both the predator and edible prey decline in the presence of the weak interactor.

Noonburg and Abrams (2005) have recently questioned the applicability of this prediction to systems experiencing transient dynamics. Using models of a single predator feeding on two prey, they show that presence of predator-resistant species can cause long transient periods of low predator and edible-prey abundance. Thus, prey heterogeneity can reduce stability by enhancing extinction probability and decreasing the probability of predator-mediated coexistence of competing prey. This destabilizing effect was found to increase greatly with increasing levels of system enrichment. Thus, the capacity of predator-resistant prey to temper the paradox of enrichment is reversed during transient phases. These predictions have important implications for many natural systems whose dynamics are best characterized as transient (e.g., temperate-zone planktonic systems), yet they have not been demonstrated experimentally. We used a laboratory-based planktonic predator-prey system to explore the interactive effects of nutrient enrichment, dilution rates, and the presence/absence of defended prey on transient dynamics. We first parameterized a model of our system to identify treatment levels that generated distinct dynamic outcomes and then tested predictions using a controlled laboratory experiment. Our findings show that the presence of weak interactions can have contrasting effects on predator-prey dynamics, stabilizing some features of these systems and strongly destabilizing others under some conditions.

MODEL METHODS

We developed a model of our experimental system to examine how inedible prey affect extinction probability of predators and their edible prey during transient phases. We also explored how these effects varied with nutrient enrichment and dilution rates under chemostat conditions. Our laboratory aquatic system was composed of the rotifer *Brachionus calyciflorus* as a top predator, the unicellular green alga *Ankistrodesmus falcatus* as its edible prey and the unicellular alga *Cosmarium* (unknown sp.) as the weakly interacting prey species. All species are hereafter referred to by genus. Due to its large size *Cosmarium* is completely inedible by the predator; mean biovolume per cell of *Cosmarium* measured in log growth phase is $17\,203\ \mu\text{m}^3$ (average dimensions, $54 \times 46\ \mu\text{m}$) vs. $131\ \mu\text{m}^3$ for *Ankistrodesmus* (average dimensions, $54 \times 1.5\ \mu\text{m}$). *Cosmarium*, while defended from predation, is a poor resource competitor for phosphorus compared to *Ankistrodesmus* as revealed by growth kinetics (Appendix A: Fig. A1) and mutual invasibility trials under different nutrient concentrations (Appendix B: Fig. B1). Thus, weak trophic interactions are expressed in the system via *Cosmarium*'s exploitation of resources (as in McCann et al. 1998: Fig. 1B). To produce predictions specific to our study system, we first parameterized a mechanistic model of our laboratory

food web. Our model was similar in structure to Noonburg and Abrams (2005), with the following modifications that we made to better match the biology of our system: (1) chemostat conditions to model nutrient renewal and background mortality, (2) type II functional responses of predators and prey, and (3) removal of the feeding link between the top predator and the defended prey, as *Cosmarium* was inedible. Model parameterization is detailed in Appendix A. We modeled interactions using the following equations:

$$\frac{dZ}{dt} = g(P_{\text{ed}})cZ - IZ \quad (1)$$

$$\frac{dP_{\text{ed}}}{dt} = f_{\text{ed}}(N)P_{\text{ed}} - IP_{\text{ed}} - g(P_{\text{ed}})Z \quad (2)$$

$$\frac{dP_{\text{in}}}{dt} = f_{\text{in}}(N)P_{\text{in}} - IP_{\text{in}} \quad (3)$$

$$\frac{dN}{dt} = I(N_{\text{conc}} - N) - f_{\text{ed}}(N)\frac{P_{\text{ed}}}{b_{\text{ed}}} - f_{\text{in}}(N)\frac{P_{\text{in}}}{b_{\text{in}}} \quad (4)$$

where N is a limiting nutrient (phosphorus), Z is predator density, and P_{ed} and P_{in} are densities of the edible and inedible prey, respectively. We assumed chemostat conditions with a constant dilution rate (I) and a concentration N_{conc} of incoming nutrients. Predator feeding ($g(P_{\text{ed}})$) was modeled with a Holling type II functional response:

$$g = \frac{aP_{\text{ed}}}{1 + ahP_{\text{ed}}} \quad (5)$$

where a is an attack rate and h the handling time per prey. When observing *Brachionus* feeding behavior we found that *Cosmarium* was too large to enter the feeding apparatus of the predator. Hence, we assume that the defended prey does not interfere with predator feeding on the edible alga. Edible and inedible prey nutrient uptake and growth $f_{\text{ed}}(N)$ and $f_{\text{in}}(N)$, respectively, were modeled using the Monod function:

$$f_i = \frac{r_{\text{max},i}N}{K_i + N} \quad (6)$$

where i is either edible (ed) or inedible (in), $r_{\text{max},i}$ is the prey's maximal growth rate, and K_i is a half-saturation constant. The conversion parameter c converted prey consumed to number of predators produced. Conversion parameters b_{ed} and b_{in} (for the edible and inedible prey, respectively) converted prey individuals to nutrients.

Transient dynamics of the system were generated numerically using mean parameter values listed in Appendix A: Table A1. We explored dynamics across a range of nutrient concentrations (N_{conc}), from $150\ \mu\text{g P/L}$ to $1600\ \mu\text{g P/L}$ at $10\text{-}\mu\text{g P/L}$ increments. We chose this range based on prior experiments that showed that the lowest and highest concentrations produced contrasting dynamics and allowed all species to persist

TABLE 1. Model predictions of the effects of the inedible prey (*Cosmarium*) on (A) short-term persistence and (B) long-term temporal variability of the predator (*Brachionus*) and edible prey (*Ankistrodesmus*) relative to systems without *Cosmarium*.

Response variable	Low dilution rate		High dilution rate	
	Low nutrient level	High nutrient level	Low nutrient level	High nutrient level
A) Transient dynamics				
Predator persistence	destabilizing (extinction 3/3)	destabilizing (extinction 1/3)	no effect (extinction 0/3)	destabilizing (extinction 0/3)
Prey persistence	no effect (extinction 0/3)	destabilizing (extinction 0/3)	no effect (extinction 0/3)	no effect (extinction 0/3)
B) Long-term dynamics				
Predator temporal variability	stabilizing (NA)	destabilizing (NA)	no effect (no effect)	destabilizing (destabilizing*)
Prey temporal variability	stabilizing (NA)	destabilizing (NA)	no effect (no effect)	stabilizing (destabilizing*)

Notes: Predictions are shown for dilution rates and nutrient levels matching those used in the experiment. Experimentally observed effects of *Cosmarium* presence/absence are shown in parentheses. Observed transient dynamic responses are expressed as the number of replicates out of three exhibiting extinctions. Long-term dynamic responses were based on pairwise comparisons between treatments of temporal variability. "NA" indicates treatments where data were not available due to predator extinctions. * $P < 0.05$.

depending on the presence/absence of the inedible prey. Our pilot experiments also indicated that dynamics transitioned from an extinction-prone to persistent system between dilution rates of 10% and 25% per day under semi-continuous culture. Therefore we also explored the effects of dilution rate (I), numerically generating transient dynamics at instantaneous rates of 0.11 and 0.29 per day (equivalent to 10% and 25% removal once per day under semi-continuous conditions). To examine effects of the presence/absence of weak interactions, all nutrient concentrations and dilution-rate combinations were run with either the inedible prey present or absent. All simulations were run using low initial densities of each population (Appendix A: Table A1). In our experiments *Brachionus* were invaded four days following inoculation of phytoplankton to minimize demographic stochasticity due to low initial resource densities. We ran simulations using both simultaneous invasion of all three species and invasion by *Brachionus* delayed by four days; results were almost indistinguishable. Thus, we present results for the delayed *Brachionus* invasion simulations only.

For the parameter values and range of environmental conditions explored, all simulations produced an initial peak and decline in abundances of the predator and edible prey. Thus, we measured extinction probability during initial transient dynamics by examining the minimum density following the first population peaks of the predator and edible prey (as an inverse measure of susceptibility to extinction). As a basis of comparison with previous studies, we also examined long-term dynamic attractors calculated over days 15 000–20 000 from our numerical output. Simulations and analyses of dynamics were performed using Matlab Version 7.9 (Mathworks 2009).

MODEL RESULTS

Qualitative predictions of the effects of the presence/absence of inedible prey on short-term and long-term

stability of the predator and edible prey are given in Table 1 (for nutrient levels and dilution rates equivalent to those used in the experiment). When examining short-term transient dynamics, our model results were qualitatively similar to those of Noonburg and Abrams (2005). Presence of the inedible prey generated a long phase of low predator and edible-prey abundance following initial increases in population size (see Appendix B: Fig. B2 for example dynamics). Increasing system enrichment decreased minimum population abundances of the predator and edible prey regardless of the presence or absence of the inedible prey (Fig. 1). However, presence of the inedible prey interacted with the destabilizing effects of enrichment by greatly increasing the time period between transient population oscillations (Appendix B: Fig. B3) and depressing minimum predator and edible-prey abundances when compared to food chains without the inedible prey (Fig. 1A, C). Effects of the inedible prey on minimum population sizes were most pronounced for the predator in which abundances following initial population peaks were depressed by several orders of magnitude compared to systems without the inedible prey (Fig. 1C). Thus, presence of weak trophic interactions greatly increased the probability of predator extinction during initial transient oscillations especially at high levels of enrichment. Our model also revealed that increasing the dilution rate to the system dampened the destabilizing effects of prey heterogeneity by delaying initial invasion of the inedible prey (Appendix B: Fig. B2), which reduced the time between transient oscillations (Appendix B: Fig. B3) and increased minimum densities of both the predator and edible prey (Fig. 1B, D).

As a basis of comparison with previous studies, we also examined long-term dynamic attractors from our numerical output (Appendix B: Figure B4). At the low end of the nutrient gradient, predator and edible prey exhibited stable point equilibria in the presence or absence of the inedible prey. Increasing nutrient

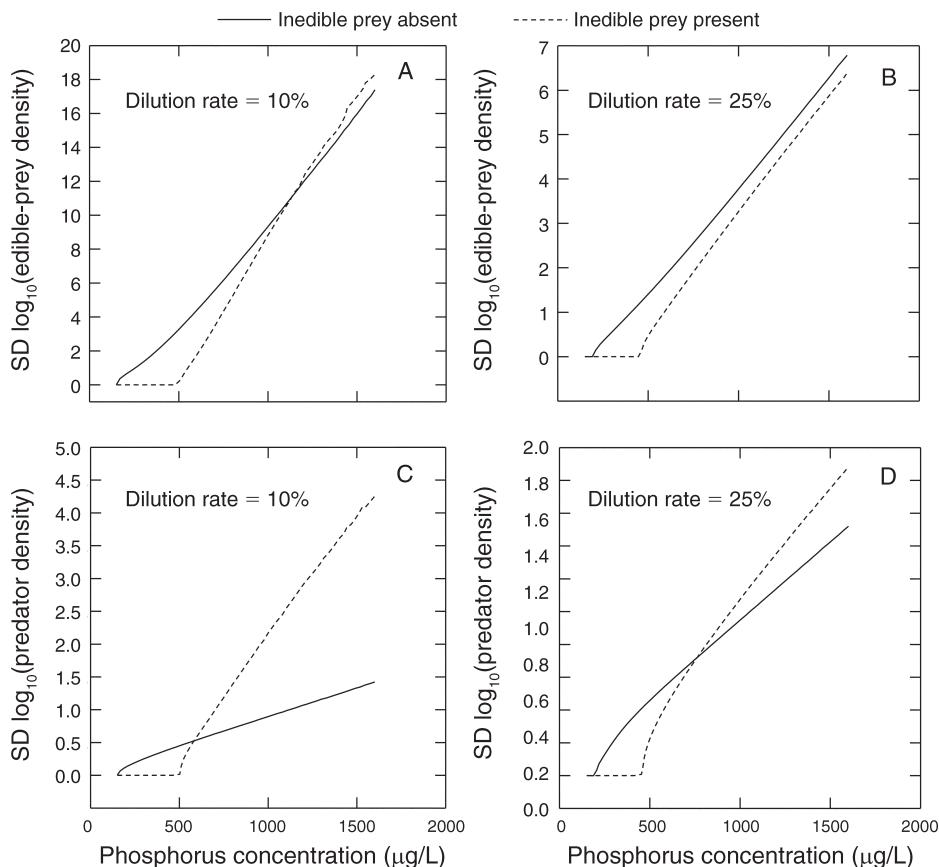


FIG. 2. Model predictions of the effects of enrichment, weak trophic interactions (inedible-prey presence/absence), and dilution rate on temporal variability of long-term dynamic attractors of (A) the edible prey at a 10% per day dilution rate, (B) the edible prey at a 25% per day dilution rate, (C) the predator at a 10% per day dilution rate, and (D) the predator at a 25% per day dilution rate. Variability was measured as the standard deviation of \log_{10} -transformed densities over days 15 000–20 000 of the simulations. Lines are cubic spline fits through model data points. Density was originally measured as number/mL.

concentrations produced paradoxical enrichment dynamics of the predator and edible prey, with both exhibiting limit cycles of increasing amplitudes. However, we found only partial support for a stabilizing effect of weak trophic interactions over this nutrient range. Presence of the inedible prey moved systems from limit cycles to stable point equilibria at the lower end of this portion of the enrichment gradient (Appendix B: Fig. B4). At a limited range of intermediate levels of enrichment, presence of the inedible prey did not produce stable point equilibria but reduced the amplitude of population cycles, reducing maximum densities and increasing minimum densities of both the edible prey and the predator (Appendix B: Fig. B4). However, at higher levels of enrichment, presence of the inedible prey strongly decreased population cycle minima of the edible prey and especially of the predator for which extinction probability was greatly enhanced regardless of dilution level (Appendix B: Fig. B4). These effects were reflected when examining temporal variability of the predator and edible prey (Fig. 2), measured as the standard deviation of \log_{10} -transformed densities over

days 15 000–20 000 of the simulations (densities were measured at one-day intervals as in our experiment). At the low dilution rate, presence of the inedible prey stabilized systems at low to intermediate levels of enrichment and destabilized populations at higher nutrient levels (Fig. 2A, C). Increasing the dilution rate weakened the destabilizing effects of the inedible prey on the predator and shifted the effect from destabilizing to stabilizing for the edible prey (Fig. 2B, D).

EXPERIMENTAL METHODS

To test model predictions (Table 1) we performed a laboratory experiment using our model planktonic system. We obtained cultures of the rotifer *Brachionus calyciflorus* from Florida Aqua Farms (Dade City, Florida, USA) and the unicellular alga *Cosmarium* from Carolina Biological Supply (Burlington, North Carolina, USA) and *Ankistrodesmus falcatus* from A. J. Tessier (Michigan State University, East Lansing, Michigan, USA). *Brachionus* stock cultures were fed *Ankistrodesmus* and all cultures were maintained using the same environmental conditions as in the experiment.

Experimental vessels consisted of 500-mL flasks filled with 400 mL of COMBO medium (Kilham et al. 1998). Flasks were constantly mixed using aeration, and housed in a single environmental chamber at 25°C under 24-hour light. Flasks were randomly ordered and rotated in the chamber daily. The experimental containers were maintained as semi-continuous cultures with daily removal of a percentage of the volume and replacement with sterile medium. Additional simulations (not shown) indicated that our model predictions were qualitatively robust to changes in the mode of nutrient replacement from continuous to semi-continuous. The amount of medium replaced depended on the dilution-rate treatment imposed. Removed medium served as a zooplankton and phytoplankton sample. Although flasks were constantly mixed, we observed a light film of *Cosmarium* growing on the bottom of the flasks that contained this species. To minimize surface growth, we gently scrubbed the bottom and sides of all flasks with autoclave-sterilized stirring rods prior to our daily sampling. *Brachionus* and *Cosmarium* were enumerated using a stereomicroscope while *Ankistrodesmus* was enumerated by first obtaining a measure of total algal density using a CASY cell counter (Innovatis, Bremerhaven, Germany) and subtracting the *Cosmarium* microscope counts. As *Brachionus* males do not actively feed and were rare, population densities of *Brachionus* were based only on counts of females. All experimental materials were autoclave sterilized prior to use.

As our intent was not to experimentally identify bifurcations and transition points between dynamic behaviors, we instead used a factorial design to explore the interactive effects of dilution rate, nutrient enrichment, and prey heterogeneity on predator-prey dynamics. We used a $2 \times 2 \times 2$ factorial design with two dilution rates (10% vs. 25% replacement per day) crossed with presence vs. absence of *Cosmarium* crossed with two levels of phosphorus enrichment (160 $\mu\text{g P/L}$ vs. 1600 $\mu\text{g P/L}$). Phosphorus levels spanned the range used in our numerical analysis and were predicted to generate contrasting transient dynamics and long-term dynamic attractors (Table 1). All other nutrients, vitamins, and trace elements were provided at nonlimiting concentrations equal to standard COMBO medium concentrations. Dilution rates and initial densities of all species matched those used in the numerical analysis (Appendix A: Table A1). Both phytoplankton species were added simultaneously (day 0) and allowed to grow for four days at which time *Brachionus* were added to the flasks. All treatment combinations were replicated 3 times and flasks were sampled daily beginning on day 6 and ending on day 66. One replicate flask of the high-nutrient, low-dilution-rate, *Cosmarium*-present treatment cracked on day 44 due to human error. We attempted to transfer the contents of the container to a new sterile flask. However, this appeared to have a strong impact on population dynamics (Appendix B: Fig. B5I). Statistical analyses were performed using Systat Software (2009).

EXPERIMENTAL RESULTS

Qualitative model predictions of the effects of *Cosmarium* presence/absence and corresponding experimental results are summarized in Table 1. Examining short-term population dynamics, our model predicted the strongest effects of the inedible prey on extinction probability for the predator at the low dilution rate (Fig. 1C). In our experiment, presence of the inedible prey, *Cosmarium*, increased extinctions of *Brachionus* in the low-dilution treatments. Both the predator and edible prey persisted for the duration of the experiment in the absence of *Cosmarium* (Fig. 3B, D), in contrast to systems that included the inedible alga (Fig. 3A, C). In the low-nutrient treatment, *Brachionus* rapidly fell below sampling detection limits following its first population oscillation in all replicates with the inedible prey (Fig. 3A). After five consecutive days of zero sample densities, we exhaustively sampled the entire volume of each replicate flask and confirmed predator extinction in all cases. Our model also predicted that extinction probability should increase with increasing nutrient enrichment, especially in the presence of *Cosmarium* at low dilution rates (Fig. 1). While we observed predator extinctions in the high-nutrient, low-dilution treatment with *Cosmarium*, rapid extinction of *Brachionus* only occurred in a single replicate—again following the first population oscillation (Fig. 3C). However, the predator persisted for 56 days in one replicate, exhibiting highly variable abundances before falling below sampling detection; extinction was verified after five days of zero values (Appendix B: Fig. B5G). In the third replicate, *Brachionus* persisted until the termination of the experiment, although its densities were highly variable and often fell to extremely low levels (Appendix B: Fig. B5I). As previously noted, however, this replicate had to be transferred to a new flask at day 44. Hence, dynamics after this day must be viewed with caution. *Brachionus* persisted in all replicates of the high-nutrient, low-dilution treatment in the absence of *Cosmarium* (Fig. 3D; Appendix B: Fig. B5).

As predicted by our model, increasing the dilution rate of the system moderated the destabilizing effects of *Cosmarium* by weakening the invasion of the inedible prey and promoting *Brachionus* persistence in all replicates of the low and high nutrient level treatments (Fig. 4A, C; Appendix B: Fig. B5). Although *Cosmarium* densities were much lower at these higher flushing rates, it did invade and persist in all replicates for the duration of the experiment.

When analyzing long-term dynamic attractors, our model produced contrasting predictions of the effects of the inedible prey on predator-prey stability (Table 1, Fig. 2). Focusing first on the low-dilution-rate treatments, our model predicted that predator and edible prey would exhibit limit cycles in the absence of the inedible prey in our low-nutrient treatment, with the amplitude of the cycles (and temporal variability) increasing in our high-nutrient treatment (e.g., Fig.

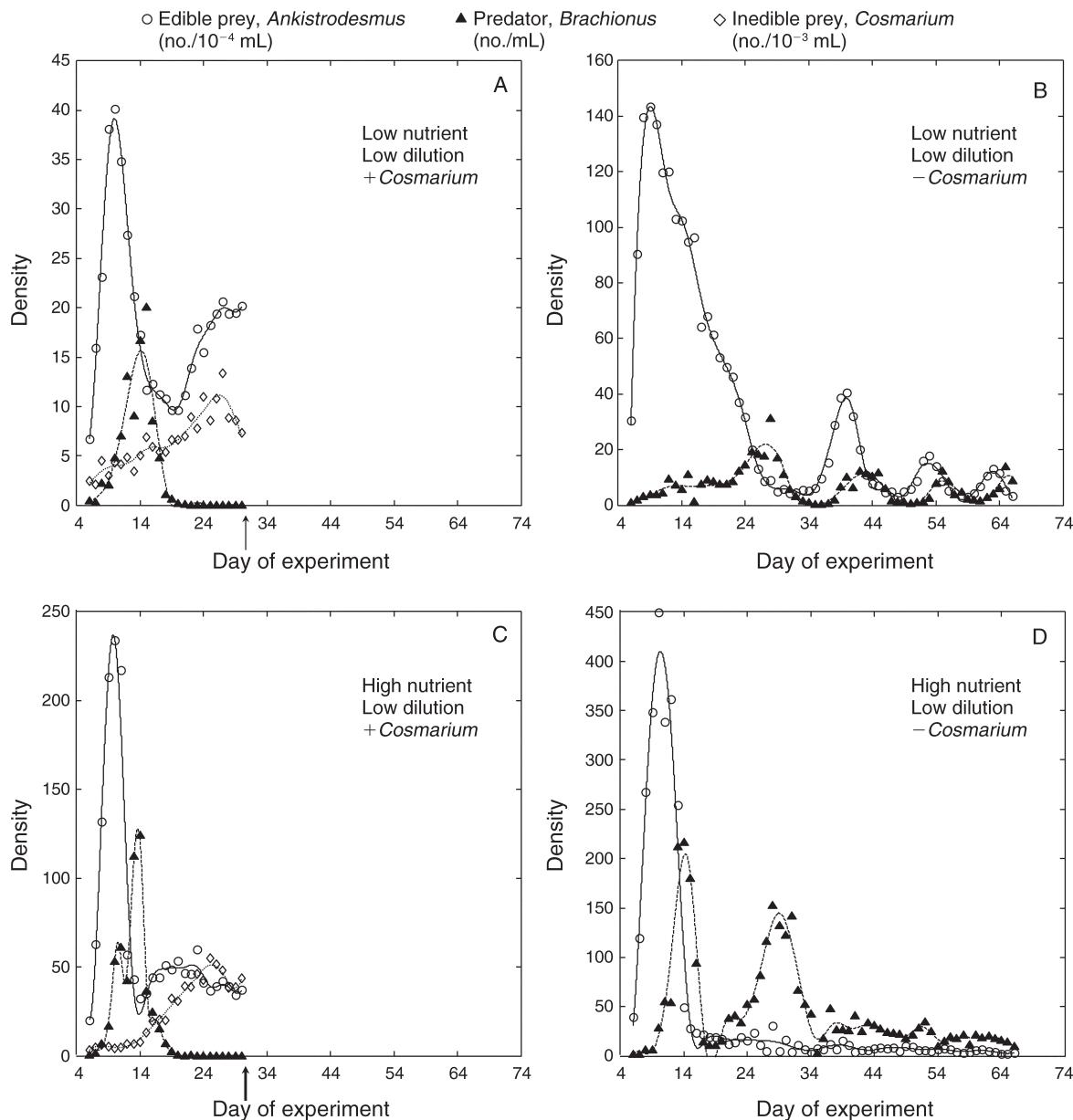


FIG. 3. Example experimental dynamics of the edible prey (*Ankistrodesmus*), the predator (*Brachionus*), and the inedible prey (*Cosmarium*) in the low-dilution-rate treatment. Dynamics for all replicates can be found in Appendix B: Fig. B5. (A, B) Dynamics in the presence or absence of the inedible prey at the low nutrient level and low dilution rate; the arrow in panel (A) indicates the day of confirmed predator extinction. (C, D) Dynamics in the presence or absence of the inedible prey at the high nutrient level and low dilution rate; the arrow in panel (C) indicates the day of confirmed predator extinction. Densities have been rescaled. Lines are penalized regression splines fit using cross-validation parameter selection (Shertzer et al. 2002).

2A, C). Presence of the inedible prey was predicted to stabilize both the predator and edible prey at the low nutrient level but was predicted to destabilize predator and edible prey at the high enrichment level, increasing cycle amplitudes and temporal variability (Table 1, Fig. 2A, C). Because of predator extinctions in the low-dilution treatments we could not address predicted effects of *Cosmarium* on long-term dynamics. However, in those treatments without *Cosmarium*,

predator-prey dynamics beyond initial transitory oscillations (after day 34) exhibited persistent oscillations in two of three replicates up to day 66 of the experiment at the low-nutrient level (e.g., Fig. 3B; see also Appendix B: Fig. B5D-F). In contrast, in the high-nutrient treatment, *Brachionus*-*Ankistrodesmus* dynamics appeared to be much more stable after the first two population oscillations (e.g., Fig. 3D; Appendix B: Fig. B5J-L). This was apparent when

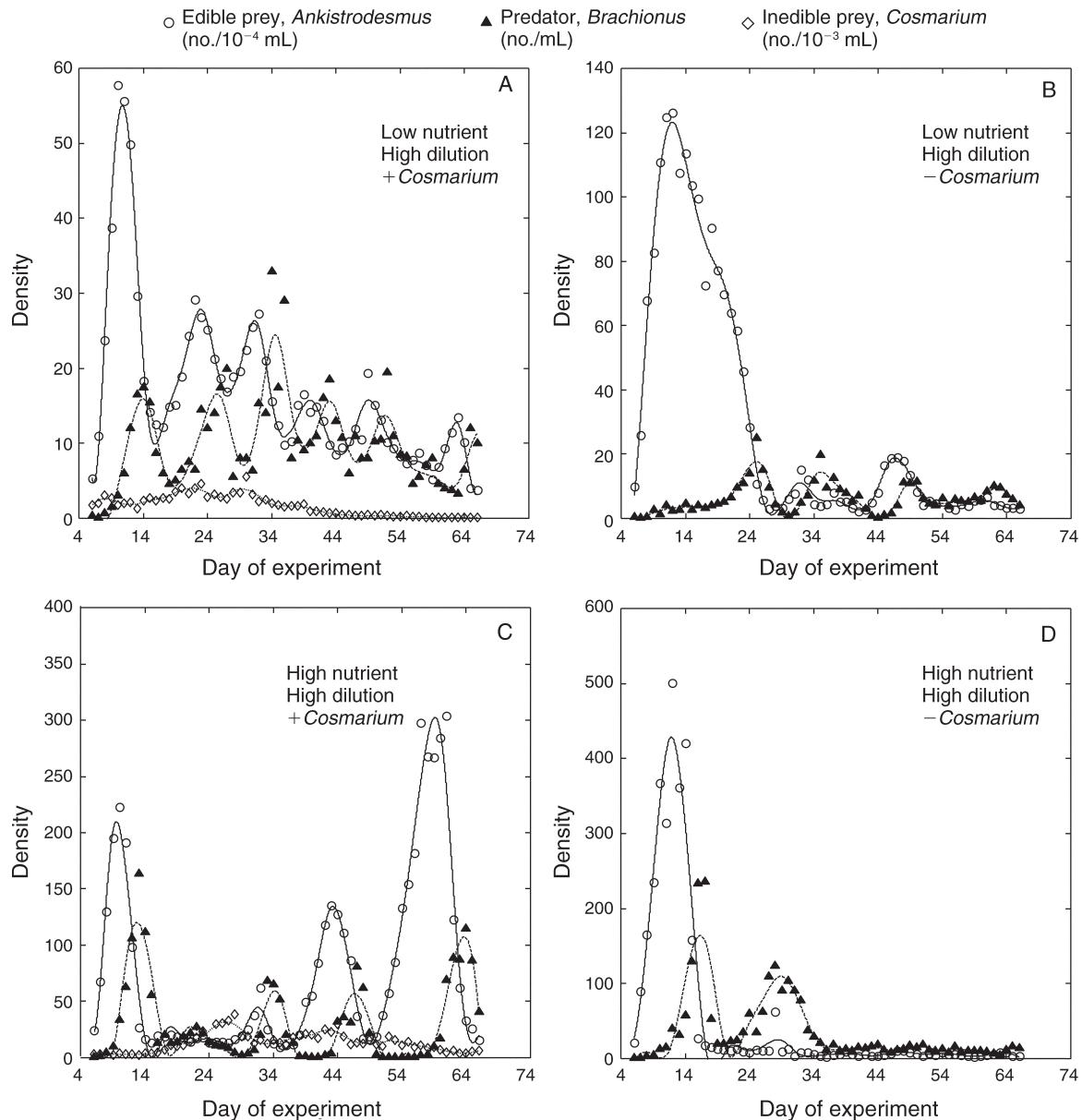


FIG. 4. Example experimental dynamics of the edible prey (*Ankistrodesmus*), the predator (*Brachionus*), and the inedible prey (*Cosmarium*) in the high-dilution-rate treatment. Dynamics for all replicates can be found in Appendix B: Fig. B5. (A, B) Dynamics in the presence or absence of the inedible prey at the low nutrient level and high dilution rate. (C, D) Dynamics in the presence or absence of the inedible prey at the high nutrient level and high dilution rate. Densities have been rescaled. Lines are penalized regression splines fit using cross-validation parameter selection (Shertzer et al. 2002).

analyzing population variability using the standard deviation of log₁₀-transformed densities over the last 32 days of the experiment: *Brachionus* was significantly less variable on average in the high nutrient treatment compared to the low nutrient treatment (Fig. 5B; $P = 0.003$, t test), whereas no difference between treatment means was present for *Ankistrodesmus* (Fig. 5A; $P > 0.30$, t test). Thus, the predator population was more stable under enriched conditions in contrast to model predictions.

Turning to long-term dynamics in the high-dilution-rate treatments, our model predicted that the edible prey and predator should exhibit damped oscillations toward stable equilibria in the low-nutrient treatment. Hence, presence of the inedible prey should have no effect on temporal variability of the predator or edible prey (Fig. 2B, D, Table 1). In the high-nutrient treatment, our model predicted that *Brachionus* and *Ankistrodesmus* would exhibit limit cycles; thus, temporal variability was predicted to increase with enrichment in the absence of

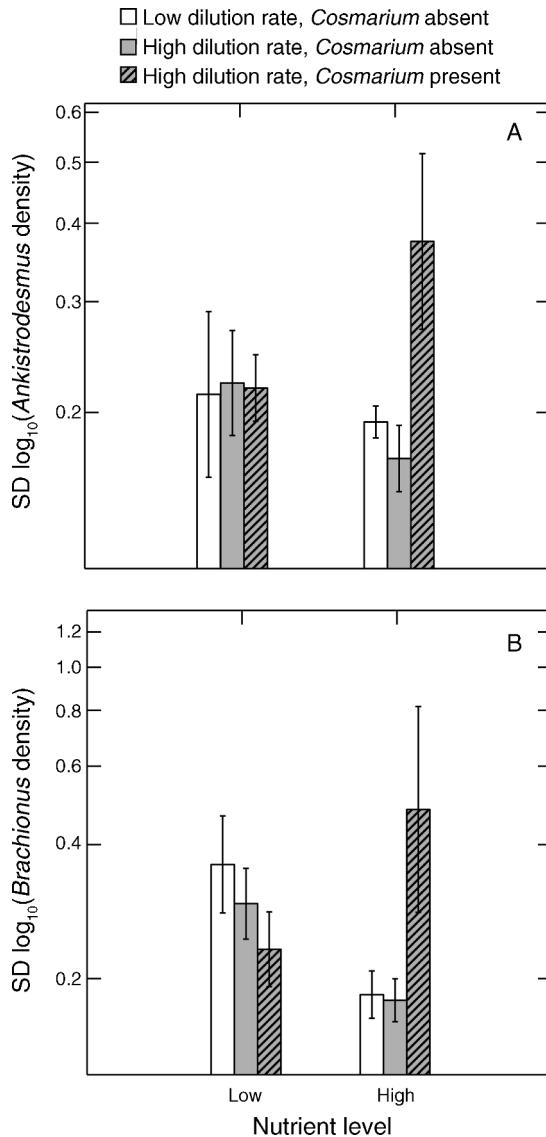


FIG. 5. Effects of nutrient level, dilution rate, and *Cosmarium* presence/absence on temporal variability of (A) *Ankistrodesmus* and (B) *Brachionus* populations measured over the last 32 days of the experiment (shown are means \pm SE across replicates of each treatment). Variability was measured for each replicate as the standard deviation (SD) of log₁₀-transformed densities after day 35. Density was originally measured as number/mL. Results for low-dilution-rate treatments with *Cosmarium* present were not calculated due to extinctions.

Cosmarium (Fig. 2B, D). Presence of *Cosmarium* under high enrichment was predicted to further destabilize *Brachionus*, increasing cycle amplitudes and temporal variability (Fig. 2D), but was predicted to have a weak stabilizing effect on *Ankistrodesmus* (Fig. 2B). When examining our experimental results over the last 32 days of the experiment, *Brachionus* and *Ankistrodesmus* variability appeared to decrease, not increase, when comparing means in the low- and high-nutrient treat-

ments in the absence of *Cosmarium* (Fig. 5A, B), in contrast to model predictions. As predicted by our model, presence of *Cosmarium* increased the temporal variability of the predator under high enrichment (Fig. 5B). However, *Cosmarium* did not stabilize *Ankistrodesmus* populations at high enrichment as predicted; instead population variability of *Ankistrodesmus* also increased in the presence of the inedible prey (Fig. 5A). ANOVA of standard deviations of log₁₀-transformed densities revealed a significant interaction between nutrient enrichment and *Cosmarium* presence/absence for both *Brachionus* ($P = 0.028$, $F_{1,8} = 7.13$) and *Ankistrodesmus* ($P = 0.031$, $F_{1,8} = 6.79$) in the high-dilution-rate treatments. For both species the presence of *Cosmarium* increased temporal variability in the high-nutrient treatment ($P < 0.05$, Tukey's HSD, pairwise comparisons) but had no effect at low-nutrient enrichment ($P > 0.19$, Tukey's HSD, pairwise comparisons).

DISCUSSION

Assumptions of timescale and dynamic state are key components of any theoretical exploration, determining the extent of generality, applicability, and extrapolation to natural settings. As an example, assumptions of stable equilibria (often made attainable by assuming linear functional responses of species) ease attainment of analytical solutions to model formulations, providing highly generalizable model predictions (e.g., Tilman 1980, Leibold 1996). Similarly, early investigations of community stability relied on assumptions of stable point equilibria in order to facilitate numerical analyses of the effects of food-web structure on resilience (e.g., May 1973; Pimm 1982). However, such models were routinely criticized on the grounds that stable equilibria may be rare or nonexistent in natural systems and that more realistic nonlinear functional responses can often lead to unstable dynamics and model outcomes that contradict their equilibrational counterparts (Goodman 1975, McNaughton 1977, McCann 2000). This debate prompted the more recent spate of explorations focused on stabilizing mechanisms in model systems that display a broader diversity of temporal behaviors including limit cycles and chaos (McCann 2000). While such studies may hew more closely to nature, they often rely on the assumption that community dynamics have settled onto dynamic attractors. In systems that experience strong and periodic perturbations, the capacity for communities to reach dynamic attractors may be slowed or impeded. The applicability of long-term dynamic models of stability to systems displaying transient dynamics is largely unknown.

Our results show that under low dilution rates the presence of prey heterogeneity increases the extinction probability of systems experiencing transient dynamics—a finding that runs counter to the general view that weak trophic interactions stabilize predator–prey oscillations and enhance predator–prey persistence. As shown by Noonburg and Abrams (2005) and our own

model variant, the presence and initial invasion of an inedible prey can, in theory, generate long transient periods of low predator and edible-prey abundance and increased extinction probability during transient oscillations. This dynamic response is due to the combined effects of high predation pressure (following the predator's initial increase), which initially depresses edible-prey densities, and the predator-mediated invasion of the inedible prey, which delays the edible's recovery through competition for shared nutrients. This effect was predicted to be largely nullified at high rates of dilution due to reduction in the magnitude of the inedible prey's initial invasion under high mortality. Thus, a seemingly paradoxical model prediction is that stability and predator persistence during transitory phases is enhanced by increased mortality/flushing rates due to the indirect effects of diminished invasion success of the defended prey. Our experimental tests confirmed that the presence of prey heterogeneity enhanced extinction probability of the predator *Brachionus*. At the low dilution rate the presence of the inedible alga, *Cosmarium*, induced rapid *Brachionus* extinctions in all replicates of the low nutrient treatment and in one of three replicates of the high-nutrient treatment (with delayed extinction in a second replicate). This outcome contrasted clearly with the corresponding controls without *Cosmarium* in which *Brachionus* populations persisted for the length of the experiment. As predicted, increasing dilution rates weakened *Cosmarium* invasion and enhanced *Brachionus* persistence at both low and high nutrient-enrichment levels.

In addition to impacts on transitory dynamics, our model also revealed contrasting effects of weak trophic interactions on long-term dynamic attractors. Consistent with prior studies, we found a stabilizing effect of inedible prey on predator-prey stability—moving systems from limit cycles to stable point equilibria or reducing the amplitude of population cycles at higher levels of enrichment. However, stabilizing effects only emerged at low to intermediate levels of enrichment. At higher levels of nutrient input, presence of the inedible prey greatly decreased the minimum densities of both predator and edible-prey population cycles, increasing temporal variability and extinction probability. While it may be questionable whether our experimental duration was long enough to attain long-term dynamic attractors, examination of predator-prey dynamics over the last half of the experiment revealed several intriguing patterns that qualitatively supported some of these predictions. In the high-dilution-rate treatment, our model predicted weak or nonexistent effects of *Cosmarium* on predator and edible-prey temporal variability under low enrichment, and a strong destabilizing effect on predator dynamics under high enrichment (Fig. 2B, D). Indeed, in our low nutrient treatments the presence of *Cosmarium* had no effect on temporal variability of *Ankistrodesmus* or *Brachionus* populations (Fig. 5). In contrast, presence of *Cosmarium* greatly

increased temporal variability of *Brachionus* in the high enrichment treatments, as predicted by our model (Fig. 5). Interestingly, *Ankistrodesmus* also exhibited increases in variability in the presence of *Cosmarium* at high enrichment, in contrast to our model that predicted a weak stabilizing effect of the inedible prey.

Some additional departures from general model predictions were apparent in our experiment (Table 1). Both Noonburg and Abrams (2005) and our model predicted that the effects of defended prey on predator extinction probability would increase greatly with enrichment under low dilution rates. Instead, *Brachionus* exhibited rapid extinction in only one of three high-nutrient replicates and delayed extinction in the second. In the third, the predator persisted for the duration of the experiment. The incongruence between predictions and observations suggests a need for further model development to attain stronger agreement between models and experimental dynamics. However, with only three replicates per treatment, we must also consider the possibility that limited replication likely hindered our ability to detect effects on predator-prey extinctions—a general weakness in our study. As extinction probability was empirically assessed as the proportion of replicates in which extinction was observed, greater replication would have increased our capacity to quantify extinction responses and ascribe confidence in perceived differences between treatments.

Also absent in our experiment was any paradox of enrichment dynamics in the absence of the inedible prey. Our model predicted that both the predator and edible prey should exhibit large increases in cycle amplitudes and extinction probability when comparing our low- and high-enrichment treatments. In contrast, temporal variability of *Brachionus* and *Ankistrodesmus* beyond initial oscillations was either unaffected or decreased with increasing enrichment in the absence of *Cosmarium*. Although this result seems paradoxical in itself, it closely mirrors those of Kirk (1998) in which a similar rotifer-algal system produced a “reverse paradox of enrichment” where predator dynamics were less variable under enriched prey conditions. Kirk (1998) attributed this result to density-dependent mortality of the predator induced by the production of an unknown autotoxin—a mechanism that can theoretically counter the destabilizing effects of enrichment (Murdoch et al. 1998). While autotoxin production is a plausible explanation for our patterns, more recent studies have also shown that rapid prey evolution and intraspecific heterogeneity in edibility can have profound effects on predator-prey dynamics (Schertzer et al. 2002, Yoshida et al. 2003, 2007, Hairston et al. 2005, Meyer et al. 2006, Jones and Ellner 2007). There are multiple lines of evidence that indicate that this mechanism may not account for our reverse paradox of enrichment in the absence of the inedible prey. First, both models and experiments using *Brachionus*-algae and phage-bacteria systems have shown that rapid prey adaptation can result in cryptic prey cycles in which

predators continue to oscillate and total prey abundance is stabilized as edible and predator-resistant prey phenotypes oscillate out of phase of each other (Bohannan and Lenski 1997, Jones and Ellner 2007, Yoshida et al. 2007). Such dynamics are predicted to be strongly expressed when predator resistance is effective but not overly costly to the defended morph (Jones and Ellner 2007, Yoshida et al. 2007). We observed no strong support for such differential dynamic responses in our experiment. For all treatment combinations in Fig. 5, temporal variability of *Ankistrodesmus* did not differ significantly from *Brachionus* (all $P > 0.13$, paired t tests, P values not adjusted for multiple comparisons); the lone exception was the low-nutrient, low-dilution-rate treatment in which *Brachionus* was more variable than the edible prey ($P = 0.016$, paired t test, P value not adjusted for multiple comparisons). Alternatively, when cryptic cycles do not emerge, prior work has shown that rapid prey adaptation can induce predator oscillations that are almost completely out of phase with prey oscillations (Schertzer et al. 2002, Yoshida et al. 2003, Jones and Ellner 2007)—in contrast to simple, non-evolutionary models of predator–prey dynamics that predict quarter-period phase lags. We found no clear evidence of out-of-phase cycles between *Brachionus* and *Ankistrodesmus* in treatments lacking *Cosmarium*; when oscillations were evident, they exhibited classic quarter phase lags between the predator and edible prey (Figs. 3 and 4).

While cryptic cycles due to rapid adaptation may not account for population-level stability of *Ankistrodesmus* in our experiment, such dynamic predictions are also applicable at the community level. Hence, in treatments with the inedible prey, asynchronous oscillations between *Ankistrodesmus* and *Cosmarium* could have stabilized total prey abundance over time. When examining prey–population covariation over time in the high-dilution-rate treatments, we found some evidence of asynchronous population oscillations over the last 32 days of the experiment. In the low-nutrient treatment, correlations between *Ankistrodesmus* and *Cosmarium* populations were on average positive but not significantly different from zero ($P > 0.10$, one-sample t test). In contrast, correlations between prey in the high-nutrient treatment were on average negative and significantly different from zero ($P = 0.01$, one-sample t test). While asynchrony could have reduced temporal variability of total prey abundance, no effect was detected. There was a trend for reduced temporal variability of total prey biovolume in the presence of *Cosmarium* in the high-nutrient treatment (Appendix B: Fig. B6), but the effect was not statistically significant ($P = 0.56$, t test). This is perhaps not surprising as *Cosmarium* inedibility was paralleled by a strong reduction in competitive ability relative to *Ankistrodesmus*. As alluded to above, cryptic cycles are only predicted for cases where defense against predators comes at a small cost in competitive ability (Jones and Ellner 2007, Yoshida et al. 2007).

Although our model system is by necessity a highly simplified caricature of nature, application of our qualitative predictions to natural systems may prove fruitful. This will be most appropriate for systems that experience periodic and severe mortality events (e.g., due to seasonal environmental forcing) and where the frequency of forcing occurs on a timescale longer than population-dynamic oscillations. Moreover, our model system is based on one in which predator and prey exhibit comparable generation times. Buffering of predator population growth via long-lived stages and slow dynamic responses to periods of low resource availability would likely enhance predator population persistence during transitory phases, weakening many of our predicted effects. The most obvious parallels in nature to our experimental system are temperate planktonic communities. Such systems are known to display a strong imprint of seasonal variation on their community dynamics, with crustacean zooplankton populations commonly exhibiting only one or two oscillations during a growing season (DeMott 1989, Gliwicz and Pijanowska 1989). Thus, these dynamics are arguably best characterized as transitory rather than approaching long-term dynamic attractors within the growing season. While natural plankton communities employ strategies to maintain long-term persistence such as dormant life stages, our model could still explain many dynamic features that occur within growing seasons. For instance, patterns of planktonic succession following spring ice melt exhibit some basic features of our model results, with initial peaks in edible phytoplankton followed by peaks in zooplankton abundance that in turn are followed by increases in grazer-resistant species of algae and declines in zooplankton populations (Lampert et al. 1986, Sommer et al. 1986). This latter phase of succession is particularly strong in enriched systems. Our model suggests that increasing eutrophication can have severe effects on the timing and magnitude of such transient dynamics.

The features of natural systems that confer stability upon populations and communities remains a central question in ecology. While several studies have clearly shown that the presence of weak trophic interactions can stabilize food-web dynamics, our model and experimental results demonstrate that the presence of predator-resistant prey species can have strong destabilizing effects on both long-term and transient predator–prey dynamics, increasing population variability under enriched conditions and amplifying the probability of predator extinction during initial transient oscillations. Determining the importance and broader applicability of our findings to natural systems awaits further exploration. However, as rates of species loss, exotic species invasions, and eutrophication continue to increase, understanding the determinants of transient food-web dynamics is becoming increasingly important for predicting future impacts on the functioning and integrity of natural systems.

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SUPPLEMENTAL MATERIAL

Appendix A

A table defining parameters and variables and three figures summarizing methods and results of assays used to obtain model parameter estimates (*Ecological Archives* E093-055-A1).

Appendix B

Six figures showing results of prey invasibility assays, example model dynamics, model predictions, and population dynamics for all experimental treatments and replicates (*Ecological Archives* E093-055-A2).