

# Reports

*Ecology*, 94(4), 2013, pp. 773–779  
© 2013 by the Ecological Society of America

## Temporal dynamics of a simple community with intraguild predation: an experimental test

T. HILTUNEN,<sup>1</sup> L. E. JONES, S. P. ELLNER, AND N. G. HAIRSTON, JR.

*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA*

**Abstract.** We explore how adding complexity to a typical predator–prey interaction affects temporal dynamics. Intraguild predation webs contain competition, predation, and omnivory in a system of three species where theory and empirical results can be compared. We studied a planktonic microcosm community in which an alga is consumed by a flagellate and by a rotifer that also consumes the flagellate. Previously published theory predicts that phase lags between the species are the outcome of a “tug of war” among the intraguild-predation links: rotifers↔algae, flagellates↔algae, and rotifers↔flagellates. We observed sustained oscillations with abundance peaks that corresponded exactly to theoretical predictions in all replicates: peaks of the rotifers and flagellates fell on either side of a quarter-period lag behind the prey (algae) peaks, with the peak of the intermediate predator (flagellates) preceding that of the top predator (rotifers). The phase lags in these experiments suggest that temporal variation in flagellate growth rate is primarily driven by variation in the intensity of its consumption by rotifers, rather than by variation in the density of its algal prey. This system illustrates how interaction strength affects the pattern of intraguild predation cycles and provides an opportunity to explore how evolution of interaction strength may affect those dynamics.

**Key words:** *algae; Brachionus plicatilis; chemostat; Chlorella autophrica; flagellates; intermediate predator; laboratory microcosm; mathematical models; Oxyrrhis marina; predator–prey dynamics; rotifers; tri-trophic food web.*

### INTRODUCTION

Intraguild predation—omnivory in which a predator and its prey both consume, and potentially compete for, a common resource—has been increasingly recognized as a fundamental component of the natural food webs of a great many ecosystems (e.g., Polis et al. 1989, Polis and Holt 1992). With predation, competition and omnivory all present in a food web of just three species (Fig. 1A), this is the simplest possible embodiment of food web complexity. As such it has been an irresistible system for exploring the extent to which omnivory stabilizes food web diversity (Polis et al. 1989, Holt and Polis 1997, McCann and Hastings 1997, Vandermeer 2006).

Although much theoretical development in ecology has treated the stability and dynamics of predation and interspecific competition separately (e.g., May 1973,

Tilman 1982, 1988, Kot 2001, Murdoch et al. 2003), it is clear that in nature both processes occur simultaneously, often with strong interaction strengths (e.g., Wooton 1994, Schmitz et al. 2000, Hampton et al. 2006). Theory that explores the implications of food web complexity for community dynamics has generally been confined to analyses of stability and species persistence (e.g., May 1973, Martinez et al. 2006, Allesina and Pascual 2008), and only rarely has the nature of the underlying temporal dynamics been considered (Fussmann and Heber 2002).

In intraguild predation the top predator gains a direct energy benefit by consuming its competitor, and simultaneously reaps the indirect benefit of reducing competition for the shared resource (the prey in Fig. 1A). Stability of this system in mathematical models depends upon the magnitude of predation by the top predator on its competitor (the intermediate predator in Fig. 1A) relative to its consumption of the basal prey resource, as well as the comparative efficiencies of the top predator and the competitor in using the prey (Holt and Polis 1997, McCann and Hastings 1997, Vandermeer 2006). In predicting the dynamics of natural

Manuscript received 14 May 2012; revised 30 October 2012; accepted 13 November 2012. Corresponding editor: A. M. de Roos.

<sup>1</sup> Present address: Department of Food and Environmental Sciences/Microbiology, FIN-00014 University of Helsinki, Helsinki, Finland. E-mail: teppo.hiltunen@helsinki.fi

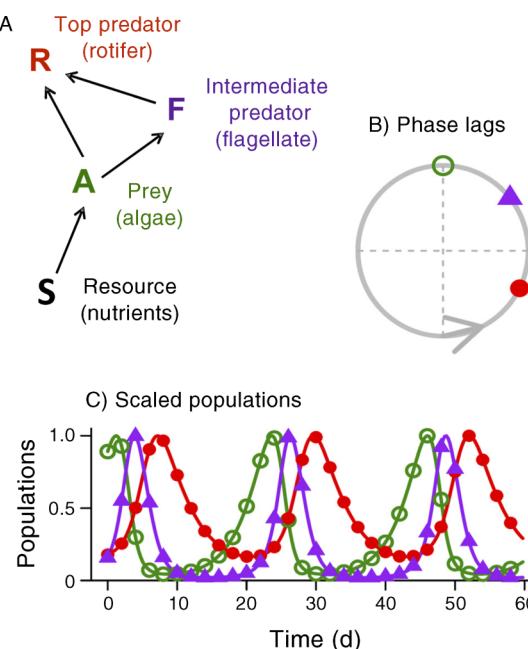


FIG. 1. (A) Structure of the three-species food web with intraguild predation found in our chemostat experiments and theoretical models. Arrows represent uptake of the nutrient substrate, S, by the prey (the alga, A, *Chlorella autotrophica*) and consumption of the prey by the intermediate predator (the flagellate, F, *Oxyrrhis marina*) and the top predator (the rotifer, R, *Brachionus plicatus*). (B, C) Theoretical predictions for the tri-trophic food web dynamics (green open circles, algae; purple solid triangles, flagellates; red solid circles, rotifers). (B) The general qualitative predictions for the phase relationship between cycle peaks in the prey, A, followed by the intermediate predator, F, and finally the top predator, R. The large circle, rotating counterclockwise, represents the tri-trophic population cycles with each species reaching its peak abundance when it comes to the top of the circle. (C) An example of the tri-trophic cycles in the model when all three species coexist (abundances for each species scaled to a maximum of 1). Parameter values:  $\delta = 0.15$ ,  $k_A = 0.15$ ,  $k_R = 0.25$ ,  $r = 0.7$ ,  $g = 0.7$ ,  $\eta = 1.5$ ,  $h = 7$ ,  $\alpha_A = 2$ ,  $\alpha_F = 1$ ,  $I_F = 0.001$ . Parameter definitions:  $\delta$  is the dilution rate (fraction of chemostat growth medium replaced each day);  $k_A$  and  $k_R$  are the half-saturation constants for algal substrate uptake and rotifer grazing, respectively;  $r$ ,  $g$ ,  $\eta$ , and  $h$  are the maximum per capita rate parameters for algal substrate uptake, rotifers grazing on algae, flagellates grazing on algae, and rotifers grazing on flagellates, respectively;  $\alpha_A$  and  $\alpha_F$  are the handling-time parameters for flagellates grazing on algae and rotifers grazing on flagellates, respectively;  $I_F$  is the rate of flagellate exogenous input.

systems, once the population parameters fall within the region that yields persistent coexistence of all species, it is also essential to understand how food web structure and interaction strengths influence the temporal patterns of population abundance. Two-species predator-prey limit cycles (locally stable periodic oscillations) are well understood, but what do the three-species limit cycles in an intraguild-predation food web look like? Because limit cycles are common in the region of coexistence for these models (Holt and Polis 1997, Vandermeer 2006),

the expected temporal pattern of abundance of the three species provides a testable prediction for what the dynamics of intraguild predation should look like in a system with real organisms.

Ellner and Becks (2011) derived a simple, general prediction for the dynamics of population cycles in a three-species system with intraguild predation: each peak in the prey should be followed first by a peak in the intermediate predator, then by a peak in the top predator. If the cycle amplitude is not too large, a more quantitative prediction is possible: the intermediate predator will lag the prey by less than a quarter of the cycle period, and the top predator should lag the prey by more than a quarter period (Fig. 1B, C; in Eq. 1 in *Methods: Intraguild predation model*, below, we present a more general version of their model and confirm that these predictions remain valid for the more general model). These predictions assume that the dynamics are not greatly affected by population structure (in particular, the cycles in the system must be consumer-resource cycles rather than delayed-feedback or other cycles driven by population age structure or stage structure [Murdoch et al. 2003]). In addition, the parameters governing the interspecific interactions must be constant; if heritable variation allows those parameters to evolve on the time scale of the population dynamics, the resulting eco-evolutionary dynamics can exhibit a wide variety of patterns (Ellner and Becks 2011).

The predicted phase lags can be interpreted as a “tug of war” among the three consumer-resource links (top↔prey, intermediate↔prey, top↔intermediate). Cycles in single-consumer-single-resource models generally exhibit a quarter-period or slightly longer lag between resource and consumer (unless cycles are modified by stage structure or evolution, as noted above). So for intraguild predation, the lag between the prey and top predator should be a quarter period if we focus on the direct link, and a half period if we focus on the indirect link via the intermediate predator. The resulting compromise is that the direct link has a longer-than-quarter-period lag, while both indirect links have lags shorter than a quarter period.

In this paper, we report the first experimental studies conducted specifically to test these predictions. The expected dynamics of a three-species system with intraguild predation were derived and published in advance of the experiments (Ellner and Becks 2011), so the results here are a genuine test of a priori predictions rather than theory created to provide a post hoc explanation of experimental results.

We studied the community dynamics of a simple laboratory microcosm of planktonic marine organisms characterized by intraguild predation in which the green alga *Chlorella autotrophica* is consumed by the flagellate *Oxyrrhis marina*, and both of these species are consumed by the rotifer *Brachionus plicatus* (see Plate 1). While theoretical explorations of three-species food webs involving all possible interspecific interactions abound

in the literature, actual experimental demonstrations of three-species population dynamics have rarely been published (an exception is Becks et al. [2005]), and we know of none with intraguild predation. Our three-species experimental microcosms provide an example of intraguild-predation dynamics highly consistent with that predicted by the mechanistic model we published previously (Ellner and Becks 2011).

## METHODS

### *Chemostat experiments*

We studied the intraguild-predation food web described above (Fig. 1A) in three continuous-culture, marine-planktonic, chemostat microcosms. Methodological details are given in Appendix A, but essential features are that each chemostat was sampled daily for between 40 and 70 days, enough time for two or three complete oscillations, following the same general methodology as in our previous studies (Fussmann et al. 2000, Yoshida et al. 2003, Becks et al. 2010). Nitrogen was the limiting nutrient, temperature was set at 21°C, and salinity was adjusted to 35 g/L. Temperature and salinity were chosen to limit somewhat rotifer growth efficiency because in preliminary experiments, under conditions more favorable to the rotifers, the flagellates were driven to extinction by rotifer predation and competition. Reported densities of the three species are averages of samples collected daily through two ports near the top and bottom of the chemostat and counted under compound (algae and flagellates) or dissecting (rotifers) microscopes.

Holt and Polis (1997) noted that the stable-limit-cycle oscillations predicted by their intraguild-predation model were often of high amplitude with a high likelihood of extinction by demographic stochasticity. Consistent with this expectation, we found that the flagellates in preliminary runs of our microcosms sometimes went extinct at the low point of a cycle. To avoid this problem, we supplemented the abundance of flagellates by continuously pumping in a low concentration of these organisms ( $\sim 10^4$  cells/d) from a separate source, amounting to 2.4% to 5.6% of the maximum concentration of flagellates in our chemostat runs. The model simulation (Fig. 1) incorporates flagellate immigration corresponding to the rate in our experiments; estimation of the immigration rate parameter is discussed in Appendix B.

Rapid evolution of algal traits conferring defense against predation has been observed to occur and to substantially change predator-prey cycling in rotifer-algal chemostats, though with different species than used here (Yoshida et al. 2003, 2007, Becks et al. 2010). In the present system, controlling prey evolution proved to be difficult. Some experimental runs were started with a single genotype of *Chlorella autrophica* to eliminate genetic variation and thereby prevent rapid prey evolution (using the same method as Yoshida et al. 2003), but evidence of prey defense evolution quickly

appeared. The direct evidence was formation of multicellular algal clumps, which has also been observed to arise as a defense against predation in other *Chlorella* species (Boraas et al. 1998). Indirect evidence was a change in population dynamics to patterns expected when the prey rapidly gain and lose a heritable defense trait in response to changes in predation intensity, notably antiphase cycles with longer period (as in Yoshida et al. 2003, Becks et al. 2010, 2012). Conversely, some experimental runs were started with multiple algal genotypes, including lineages with six months of continuous exposure to rotifer or flagellate predation, but the clumping trait quickly became and remained rare, and there was no evidence of prey defense evolution (direct or indirect) for several months, until algae from multiple lineages were added to the chemostat. Therefore, we classify experimental replicates based on the presence or absence of evidence for prey evolution, rather than by their initial genetic diversity. The data we report here are all the replicates with this experimental system that continued for at least two complete predator-prey cycles without any direct or indirect evidence of prey defense-trait evolution. Replicates with evidence for prey evolution will be reported elsewhere (T. Hiltunen, *unpublished data*).

### *Intraguild predation model*

For the case of non-evolving species, the model equations are:

$$\begin{aligned} \frac{dS}{dt} &= \delta(1 - S) - S \frac{rA}{k_A + S} \\ \frac{dA}{dt} &= A \left[ \frac{rS}{k_A + S} - \frac{gR}{k_R + A + \alpha_F F} - \frac{hF}{1 + \alpha_A A} - \delta \right] \\ \frac{dR}{dt} &= R \left[ \frac{gA}{k_R + A + \alpha_F F} + \frac{\eta F}{k_R + A + \alpha_F F} - \delta \right] \\ \frac{dF}{dt} &= F \left[ \frac{hA}{1 + \alpha_A A} - \frac{\eta R}{k_R + A + \alpha_F F} - \delta \right] + I_F \quad (1) \end{aligned}$$

with state variables  $S$  = limiting substrate,  $A$  = algae,  $R$  = rotifers, and  $F$  = flagellates, and with all parameters positive;  $\alpha$  is the handling-time parameter,  $k$  is the half-saturation constant, and  $\eta$  is the maximum per capita rate parameter for flagellates grazing on algae. These equations represent a well-mixed chemostat-type system with constant inflow of the limiting substrate and constant outflow of all species at dilution rate  $\delta$ , with all populations measured in units of limiting substrate. Eq. 1 generalizes the model of Ellner and Becks (2011) by positing a type-II functional response for feeding by, and consumption of, the intermediate predator  $F$  where Ellner and Becks (2011) assumed type-I responses ( $\alpha_F = \alpha_A = 0$ ), and by including the small influx of flagellates (at rate  $I_F$ ) that was present in the experiments reported here. Because of the type-II functional responses, the

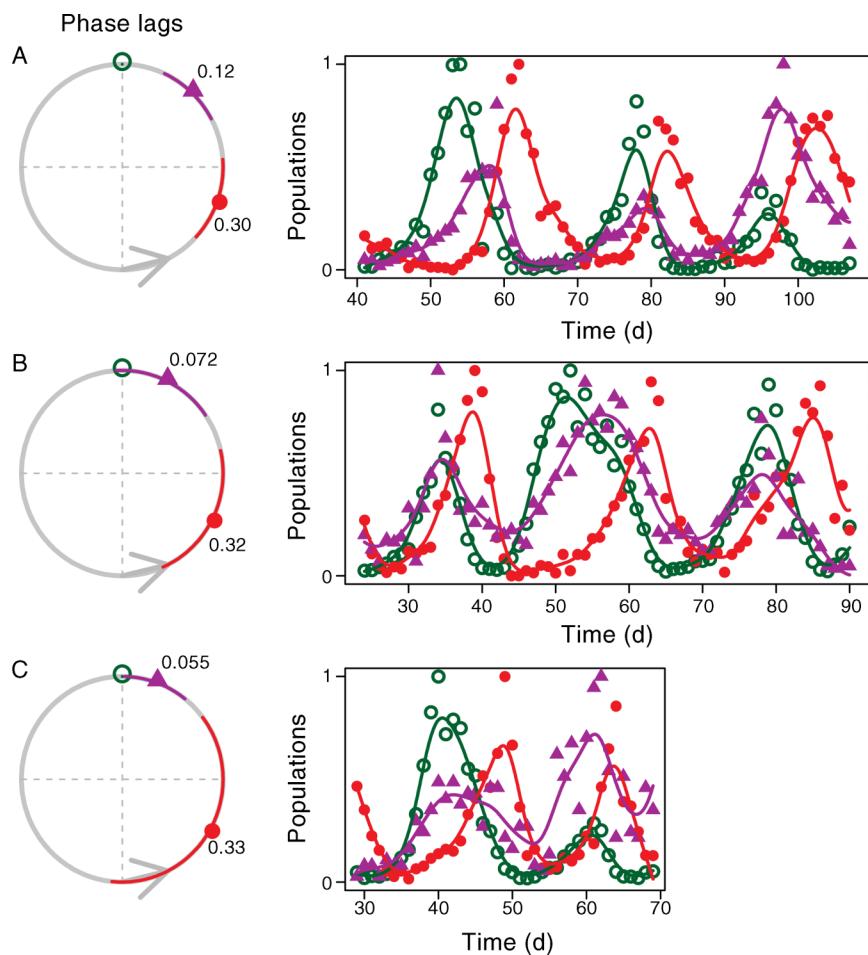


FIG. 2. Dynamics observed in three replicate chemostats with the experimental tri-trophic community. In the original data the maximum densities are: (A) algae  $1.08 \times 10^6$  individuals/mL, flagellates 3341 individuals/mL, and rotifers 9.4 individuals/mL; (B) algae  $9.9 \times 10^5$  individuals/mL, flagellates 1084 individuals/mL, and rotifers 4.8 individuals/mL; (C) algae  $1.38 \times 10^6$  individuals/mL, flagellates 472 individuals/mL, and rotifers 7.5 individuals/mL. These maximum values correspond to value 1 in the scaled populations plotted here on the right side. Symbols are the same as in Fig. 1. The larger phase-lag circles at the left, as in Fig. 1, show for each replicate the phase relationships between cycle peaks in the prey, intermediate predator, and top predator. Circle arcs associated with each symbol show  $\pm$ SE. Two methods for calculating phase lags relative to the prey are described in Appendix A, and their values ( $\pm$ SE) are given in Appendix A: Table A1.

model exhibits “paradox of enrichment” consumer-resource cycles. The population cycles predicted by the model feature successive peaks, first of the prey  $A$ , then the intermediate predator  $F$ , and finally the top predator  $R$  (Fig. 1B, C). In model simulations, peaks of the top predator typically lag behind those of the prey by more than a quarter period, while peaks of the intermediate predator lag those of the prey by less than a quarter period (Fig. 1C). This was the prediction made by Ellner and Becks (2011) based on a linearized analysis of small-amplitude cycles (in Appendix B we show that it holds also for the more general model considered here). In simulations, the prediction can fail in two circumstances. First, when the prey has very high-amplitude oscillations, with long troughs of near-zero density interrupted by brief intervals of rapid increase followed by rapid decrease; second, when the intermediate predator is

always very rare. In those situations (which did not occur in our experiments), both predator lags were shorter (relative to the cycle period) than the predictions based on small-amplitude oscillations in the three-species food web.

#### Estimating cycle period and time delays

We estimated the cycle period and the time delays between the oscillations of different species in each of the replicate experiments using two methods. One method is based on determining the elapsed time between two successive peaks based on smoothed population curves, while the second is based on the auto- and cross-correlation functions for the smoothed and interpolated data. Both methods, which give very consistent results, are described in Appendix A.

## RESULTS

After adjusting the dilution rate, salinity, and background flagellate supply rate in our chemostats so that all three species coexisted, the observed dynamics were stable limit cycles (Fig. 2). For each of the three chemostat runs, we analyzed the dynamics only for the time interval during which distinct cycling was observed, and omitted initial transient patterns observed at the start of each run (the time axes in Fig. 2 indicate the duration of the excluded transient period). In each case, the dynamics observed matched closely those predicted by theory. Our experimental food webs had periods of between 19.2 and 22.4 days (Appendix A: Table A1), which is well within the range of possible cycle periods in the model. In all three cases, the three species cycled with each peak in algal prey density followed by first by a peak in the flagellate intermediate predator, and then by a peak in the rotifer top predator (Fig. 2), exactly as predicted (Fig. 1B, C).

Theoretical analysis (Ellner and Becks 2011) showed that for cycles to occur in our model, the direct link from prey abundance to top predator population growth must be strong relative to the indirect link from prey to intermediate predator to top predator. When the direct link is very much stronger than the indirect link, the predicted lag between prey and intermediate predator peaks is substantially less than a quarter period (i.e.,  $\ll 0.25$  cycle periods), while the predicted lag between prey and top predator peaks is only slightly longer than a quarter period (i.e.,  $> 0.25$  cycle periods; see *Discussion* and Appendix B). Consistent with this prediction, we observed flagellate-algae lags of 0.055 to 0.12 cycle periods, and rotifer-algae lags of 0.304 to 0.332 cycle periods (Appendix A: Table A1). By direct microscope observations, we confirmed that the rotifers do eat the flagellate intermediate predators. The effect of the flagellate–rotifer link is also evident in the dynamics. In the absence of this link the two predators would have nearly synchronous oscillations, because their population growth rates would both vary in parallel with the fluctuating abundance of their common prey, whereas (as noted above) the observed phase lags are exactly what was predicted to occur if the flagellate–rotifer link is strong.

## DISCUSSION

The three-species, *Chlorella*–*Oxyrrhis*–*Brachionus*, intraguild-predation food web produced sustained stable oscillations with a distinct repeatable pattern of abundance peaks that corresponds exactly to our previously published theoretical predictions (Ellner and Becks 2011). Whereas in a one-predator–one-prey system the peaks in predator abundance follow those of prey abundance by a quarter of the cycle period, in our two-predator experimental system the peaks of the two predators species fell on either side of a quarter-phase lag behind the prey peaks, with the peak of the

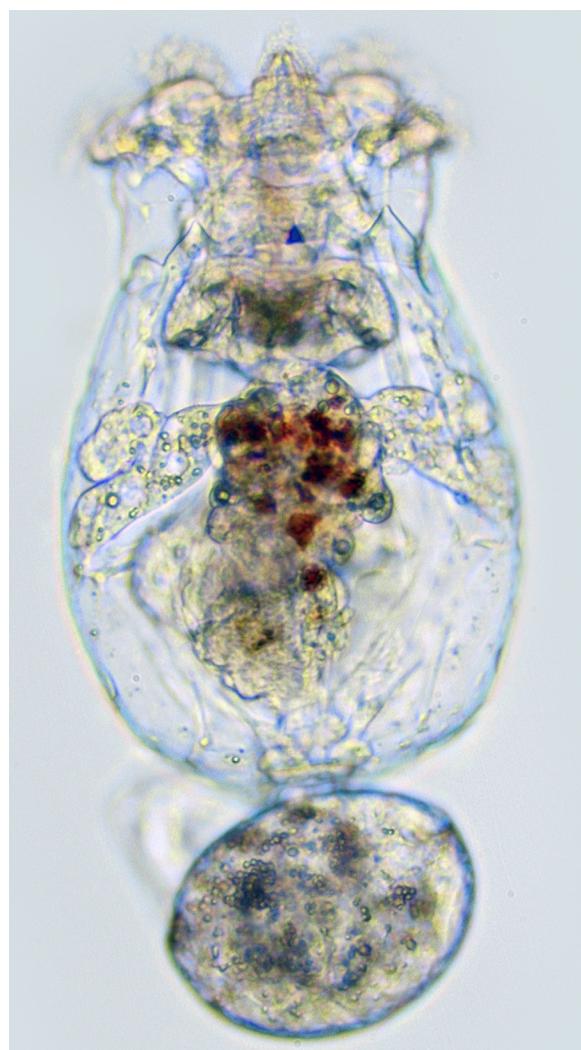


PLATE 1. The top predator in our study system, rotifer *Brachionus plicatilis*. Photo credits: Lindsay Schaffner and Kathryn Blackley.

intermediate predator preceding that of the top predator.

Our laboratory microcosm food web is reminiscent of many natural pelagic communities, where body size dominates consumer–resource interactions (Brooks and Dodson 1965, Zaret 1980): zooplankton are gape-limited but in general can consume prey that are small enough to be captured. As a result, single-celled phytoplankton are vulnerable to being eaten by both small- and large-bodied zooplankton taxa, while small-bodied grazers are also consumed by the larger ones. There are many such tri-trophic linkages in both marine and freshwater systems. Apt examples for lakes involve the dominant consumers in many water bodies worldwide. Cladocerans in the genus *Daphnia* and diaptomid copepods are relatively large planktonic crustaceans in lakes and are typically considered to be herbivores.

Both, however, have been shown to kill and consume heterotrophic flagellates, ciliates, and rotifers with which they also compete for algae (Gilbert 1985, Burns and Gilbert 1986, Williamson 1987, Williamson and Vanderploeg 1988, Pace et al. 1998).

The mean lag from algae to flagellates was  $0.092 \pm 0.034$  (mean  $\pm$  SD) of a cycle whereas the algae-to-rotifer lag was  $0.321 \pm 0.014$  (Appendix A: Table A1). Because  $(0.25 - 0.092)/(0.321 - 0.25) = 2.2$ , on average flagellates were more than twice as much below a quarter-period lag, as the rotifers were above it (Fig. 1A). For small-amplitude cycles, the analysis of Ellner and Becks (2011, Appendix B) shows that there are two situations in which the intermediate predator's lag behind the prey is very small, while the top predator's lag is above one-quarter cycle period (see Appendix B for details). The first situation occurs if the grazing pressure on the intermediate predator is potentially very large, so that even if the intermediate predator is by far the better competitor for the algal prey, grazing by the top predator keeps it from outcompeting the top predator extinct. The second situation is if the intermediate predator's functional and numerical responses to prey density are already nearly saturated during most of the population cycle. The short lags between algal and flagellate peaks in our experiments suggest that one or both of these conditions was true in our system. Either of these conditions entails that variation in flagellate population growth rate is primarily driven by variation in the per capita risk of rotifer predation, rather than by variation in the abundance of their algal prey. The natural planktonic systems mentioned previously appear to have interaction strengths consistent with this result. Pace et al. (1998) showed that although *Daphnia* and microzooplanton (flagellates, ciliates, and rotifers) all consume phytoplankton and so are potential competitors in the lakes they studied, the densities of the microzooplankton were controlled much more by *Daphnia* grazing than they were by the availability of algal resources.

A limitation of our study is that we do not have any direct information bearing on the assumption that interspecific interaction strengths are constant, in particular that there was no substantial evolution of algal traits affecting their vulnerability to predation. As noted above (see *Methods*), other experiments with this laboratory system showed both direct evidence (algal clumping) and indirect evidence (long, anti-phase cycles) that when prey defense traits were evolving they affected the dynamics. Here we have presented all chemostat runs with this three-species system for which at least two successive predator-prey cycles occurred without any such evidence of prey evolution. Additional evidence that prey evolution was not important in these data comes from the fact that two of the replicates (Fig. 2B and C) were “reseeded” with algal genetic variation just after the end of the time period studied here, by adding algae from lineages exposed to rotifer or flagellate

predation for the previous six months. In both cases, the added genetic variation led to an increase in mean algal clump size and a qualitative change in the dynamics after one or two more predator-prey cycles (T. Hiltunen, *unpublished data*). The appearance of evidence for evolution after, but not before, the deliberate introduction of heritable variation in prey defense strongly suggests that evolution played a minor role, if any, in the data sets analyzed here.

Recent theory shows that rapid predator evolution can have important effects in a system with two prey species (Schreiber et al. 2011). Tracking predator and prey trait dynamics along with species abundances may indicate when predator evolution is important. However, we did not observe any evidence that predator evolution had an important effect on temporal dynamics, nor have we in our previous studies (other than an early selective sweep in which *Brachionus calyciflorus* became obligately asexual, which is adaptive in our chemostat environment; (Fussmann et al. 2003). The reason may lie in the fact that the predators are continuously selected in our system for enhanced ability for prey consumption, sometimes strongly, sometimes weakly, whereas in contrast the direct of selection on the prey oscillates between elevated defense and increased competitive ability (and accompanying reduced defense), making prey evolution and its effect on dynamics more detectable in our system.

As noted in the *Introduction*, intraguild predation is as complex as a three-species system can be. Exploring its dynamics with and without evolution is a first step toward understanding the patterns in systems with natural levels of complexity. It is easy in mathematical models of three-species food webs, including those with intraguild predation, to find parameter combinations that lead to complex dynamics and chaos. There is evidence that chaos can occur (Becks et al. 2005) yet the existence of such dynamics in natural systems is questionable (Ellner and Turchin 1995). One question is the extent to which rapid evolution might mediate against complex dynamics in three-species food webs: for example, if dynamics are chaotic without evolution, can they be “pulled back” to limit cycles or stable coexistence by prey evolving resistance to being consumed? Alternatively, it might be that greater food-web complexity when genotypic diversity is present in prey or intermediate-predator populations “pushes” systems toward chaos. Model systems that are sufficiently complex to be reasonable caricatures of nature, as Polis et al. (1989) suggested is the case for intraguild predation, but simple enough to provide a testing ground to compare theory with empirical results, are a useful starting point—as is demonstrated here by the close match between predicted and observed dynamics.

#### ACKNOWLEDGMENTS

We thank K. Blackley, T. Hermann, A. Looi, and D. Rosenberg for help with experimental setup and sampling, and A. Barreiro, C. M. Kearns, and L. R. Schaffner for laboratory

assistance. This research was supported by grant JSMF 220020137 from the James S. McDonnell Foundation and U.S. National Science Foundation grant DEB-0813743.

#### LITERATURE CITED

- Allesina, S., and M. Pascual. 2008. Network structure, predator-prey modules, and stability in large food webs. *Theoretical Ecology* 1:55–64.
- Becks, L., S. P. Ellner, L. E. Jones, and N. G. Hairston, Jr. 2010. Reduction of adaptive genetic diversity radically alters eco-evolutionary community dynamics. *Ecology Letters* 13:989–997.
- Becks, L., S. P. Ellner, L. E. Jones, and N. G. Hairston, Jr. 2012. The functional genomics of an eco-evolutionary feedback loop: linking gene expression, trait evolution, and community dynamics. *Ecology Letters* 15:492–501.
- Becks, L., F. M. Hilker, H. Malchow, K. Jürgens, and H. Arndt. 2005. Experimental demonstration of chaos in a microbial food web. *Nature* 435:1226–1229.
- Boraas, M. E., D. B. Seale, and J. E. Boxhorn. 1998. Phagotrophy by a flagellate selects for colonial prey: A possible origin of multicellularity. *Evolutionary Ecology* 12:153–164.
- Brooks, J. L., and S. I. Dobson. 1965. Predation, body size, and composition of plankton. *Science* 150:28–35.
- Burns, C. W., and J. J. Gilbert. 1986. Direct observations of the mechanisms of interference between *Daphnia* and *Keratella cochlearis*. *Limnology and Oceanography* 31:859–866.
- Ellner, S. P., and L. Becks. 2011. Rapid prey evolution and the dynamics of two-predator food webs. *Theoretical Ecology* 4:133–152.
- Ellner, S., and P. Turchin. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. *American Naturalist* 145:343–375.
- Fussmann, G. F., S. P. Ellner, and N. G. Hairston, Jr. 2003. Evolution as a critical component of plankton dynamics. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:1015–1022.
- Fussmann, G. F., S. P. Ellner, K. W. Shertzer, and N. G. Hairston, Jr. 2000. Crossing the Hopf bifurcation in a live predator-prey system. *Science* 290:1358–1360.
- Fussmann, G. F., and G. Heber. 2002. Food web complexity and chaotic population dynamics. *Ecology Letters* 5:394–401.
- Gilbert, J. J. 1985. Competition between rotifers and *Daphnia*. *Ecology* 66:1943–1950.
- Hampton, S. E., M. D. Scheurell, and D. E. Schindler. 2006. Coalescence in the Lake Washington story: interaction strengths in a planktonic food web. *Limnology and Oceanography* 51:2042–2051.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* 149:745–764.
- Kot, M. 2001. Elements of mathematical ecology. Cambridge University Press, Cambridge, UK.
- Martinez, N. D., R. J. Williams, and J. A. Dunne. 2006. Diversity, complexity, and persistence in large model ecosystems. Pages 163–185 in M. Pascual and J. A. Dunne, editors. *Ecological networks: linking structure to dynamics in food webs*. Oxford University Press, Oxford, UK.
- May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.
- McCann, K., and A. Hastings. 1997. Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London B* 264:1249–1254.
- Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 2003. Consumer-resource dynamics. Princeton University Press, Princeton, New Jersey, USA.
- Pace, M. L., J. J. Cole, and S. R. Carpenter. 1998. Trophic cascades and compensation: differential responses of microzooplankton in whole-lake experiments. *Ecology* 97:138–152.
- Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution* 7:151–154.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.
- Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* 155:141–153.
- Schreiber, S. J., R. Bürger, and D. I. Bolnick. 2011. The community effects of phenotypic and genetic variation within a predator population. *Ecology* 92:1582–1593.
- Tilman, D. 1982. Resource competition and community stability. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D. 1988. Dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.
- Vandermeer, J. 2006. Omnivory and the stability of food webs. *Journal of Theoretical Biology* 238:497–504.
- Williamson, C. E. 1987. Predator-prey interactions between omnivorous diaptomid copepods and rotifers: the role of prey morphology and behavior. *Limnology and Oceanography* 32:167–177.
- Williamson, C. E., and H. A. Vanderploeg. 1988. Predatory suspension-feeding in *Diaptomus*: prey defenses and the avoidance of cannibalism. *Bulletin of Marine Science* 43:561–572.
- Wootton, T. J. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75:151–165.
- Yoshida, T., S. P. Ellner, L. E. Jones, B. J. M. Bohannan, R. E. Lenski, and N. G. Hairston, Jr. 2007. Cryptic population dynamics: rapid evolution masks trophic interactions. *PLoS Biology* 5(9):e235.
- Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and N. G. Hairston, Jr. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* 424:303–306.
- Zaret, T. M. 1980. *Predation and freshwater communities*. Yale University Press, New Haven, Connecticut, USA.

#### SUPPLEMENTAL MATERIAL

#### Appendix A

Detailed description of the experimental procedure and methods for analyzing the phase lags (*Ecological Archives* E094-065-A1).

#### Appendix B

Relating predator lags to interaction strengths (*Ecological Archives* E094-065-A2).