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A DIRECT, EXPERIMENTAL TEST OF RESOURCE VS. CONSUMER DEPENDENCE

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Abstract. The uptake of resources from the environment is a vital process for all organisms. Many experimental studies have revealed that the rate at which this process occurs depends critically on the resource concentration, a relationship called “functional response.” However, whether the concentration of the consumer normally affects the functional response has been the subject of a long-standing, predominantly theoretical, debate in ecology. Here we present an experimental test between the alternative hypotheses that food uptake depends either only on the resource concentration or on both the resource and the consumer concentrations. In short-term laboratory experiments, we measured the uptake of radioactively labeled, unicellular green algae (*Monoraphidium minutum*, resource) by the rotifer *Brachionus calyciflorus* (a consumer) for varying combinations of resource and consumer concentrations. We found that the food uptake by *Brachionus* depended on the algal concentration with the relationship best described by a Holling type 3 functional response. We detected significant consumer effects on the functional response only at an extraordinarily high *Brachionus* density (~125 rotifers/mL), which by far exceeds concentrations normally encountered in the field. We conclude that consumer-dependent food uptake by planktonic rotifers is a phenomenon that can occur under extreme conditions, but probably plays a minor role in natural environments.

Key words: *Brachionus calyciflorus*; functional response; Holling type 3 functional response; predator dependence; ratio dependence; rotifer.

INTRODUCTION

Functional response is the change in rate of predation by an individual predator in response to a change in density of the prey. This definition reflects the classical concept of predator–prey interactions where prey, but not predator, densities determine the rate of consumption, a view that has been challenged under the concepts of predator-dependent or ratio-dependent predation (Arditi and Ginzburg 1989, Akcakaya et al. 1995). Ratio dependence is a particular type of predator dependence in which the response only depends on the ratio of prey density to predator density. Whether predator-dependent or prey-dependent consumption prevails is an important problem in ecology because it has far-reaching implications on population dynamics. Theoretical studies have shown that the introduction of predator-dependence into predator–prey interactions causes drastic consequences for the dynamic behavior of the system (Arditi and Ginzburg 1989, Abrams 1994).

Many biologically plausible situations are conceivable where a predator's consumption rate depends on the predator concentration: e.g., density-dependent physical or social interaction among the predators,

group hunting by predators, inducible anti-predator defenses of the prey (Abrams and Ginzburg 2000). Thus, direct and indirect predator interference (mediated through the prey) is the potential mechanistic basis of predator dependence. With a clear concept at hand, the scarcity of direct, experimental tests for predator dependence is unexpected (Arditi and Akcakaya 1990, Abrams and Ginzburg 2000, Skalski and Gilliam 2001, Schenk et al. 2005). The at times heated debate between advocates and opponents of predator (and especially ratio) dependence (Diehl et al. 1993, Abrams 1994, Akcakaya et al. 1995) appears to be stuck in the exchange of largely theoretical arguments, with a thin database to back either side.

Here we present an experimental approach to the question of predator vs. prey dependence. Our study is one of the few empirical tests between these two modes of predation (e.g., Reeve 1997, Vucetich et al. 2002, Schenk et al. 2005) and the first to directly measure ingestion rates of planktonic organisms in short-term experiments over several orders of magnitudes of predator densities. Earlier experimental studies inferred predator dependence indirectly from observed plankton population dynamics (Arditi et al. 1991, Arditi and Saiah 1992, Jost and Ellner 2000), used only slightly different levels of predator density (Salt 1974, Walz and Gschloessl 1988, Mills and Lacan 2004), or the duration of the experiments was sufficiently long for

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prey depletion to occur (Salt 1974, Hayward and Gallup 1976, Helgen 1987, Hansson et al. 2001, Lüring et al. 2003). These approaches potentially introduce sources of error that our current study avoids.

We used the rotifer *Brachionus calyciflorus* (see Plate 1) and the unicellular green alga *Monoraphidium minutum* as an experimental predator–prey (consumer–resource) pair and tested between the alternative hypotheses that food uptake depends either on the resource concentration alone or on both the resource and the consumer concentrations. (Because *Brachionus* is an herbivore, we use the expressions “consumer” and “resource” instead of predator and prey, but the type of interaction is equivalent to predation). To measure consumption, we fed *Brachionus* radioactively labeled algae; the amount of radioactivity per consumer detected after the experiment is a measure of food uptake. This method is very sensitive and allows experiments of extremely short duration (4 min), thereby avoiding resource depletion during the experiment (but see Appendices A and B), a complication often associated with feeding experiments (Hansson et al. 2001, Juliano 2001, Skalski and Gilliam 2001). Short experiment duration also means that we can, a priori, exclude potential, indirect mechanisms of consumer dependence, such as induced responses in the algal resource (Lüring and Van Donk 1997) or clonal selection for favorable traits among the resource or consumer experimental populations (Fussmann et al. 2003, Yoshida et al. 2003). This is not to say that these mechanisms are unimportant in nature, but it allowed us to concentrate our analysis on the most direct type of consumer dependence: physical interference among consumers.

Our objective was to determine whether predator dependence through interference is likely to be a mechanism that affects planktonic consumers' food uptake rates at typically observed consumer densities. It is obviously true that consumption will be exclusively resource dependent if consumer density is extremely low because interference cannot occur; on the other hand, with increasingly dense packing of consumers in the pelagial, consumer dependence has to become inevitable at some point (Abrams and Ginzburg 2000). Our experimental results suggest that the threshold at which consumer dependence becomes important occurs at plankton consumer concentrations much higher than typically found in the wild.

METHODS

Feeding experiments

We used a strain of *Monoraphidium minutum* (Chlorophyta; strain 243–1, Culture Collection of Algae, University of Göttingen, Germany, mean equivalent spherical diameter = 3.5 μm) and a strain of *Brachionus calyciflorus* (mean adult lorica length = 152 μm) originally obtained by K. O. Rothhaupt. Algae were cultured in continuous-light chemostat cultures, and ro-

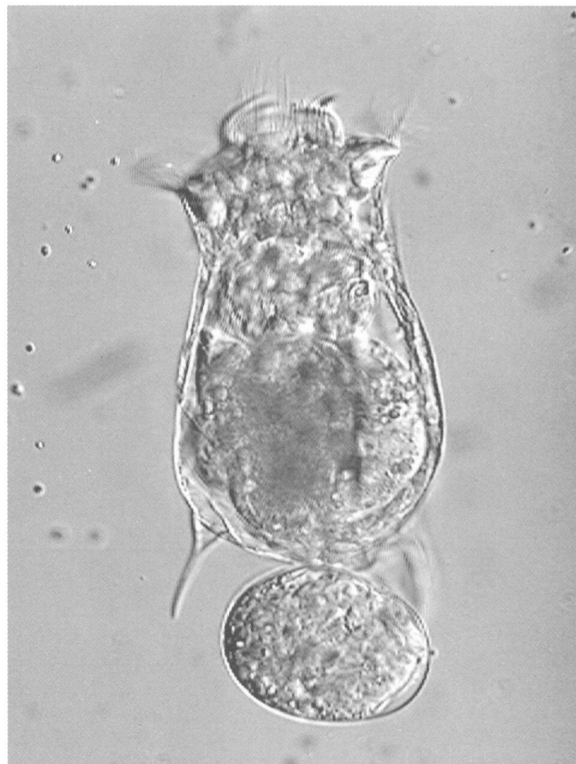


PLATE 1. Female of the rotifer *Brachionus calyciflorus* carrying an amictic egg. Photo credit: T. Yoshida and R. O. Wayne.

tifers were cultured in semi-continuous batch cultures and contained only females; for both species we used modified WC medium (Guillard and Lorenzen 1972) with a reduced inorganic nitrogen concentration of 80 $\mu\text{mol/L}$. Experiments closely followed the protocol of Rothhaupt (1990). Three days before the trials, rotifer cultures were kept at a high algal density (1×10^6 cells/mL), so that all experiments were performed with animals in the same good physiological state. Algae for experiments were harvested from chemostats on the previous day (concentration of $\sim 1.5 \times 10^6$ cells/mL), transferred to a flask, and labeled overnight with 0.37 MBq or 0.74 MBq $\text{NaH}^{14}\text{CO}_3$. Three identical flasks with unlabeled algae were set up at the same conditions (constant light, 20°C). On the morning of an experiment, we measured algal concentration in these three flasks with a CASY particle counter (Schärfe, Reutlingen, Germany), calculated the mean ($\text{cv} \leq 5.4\%$), and used this information to dilute the labeled algae to experimental concentrations.

We conducted four replicate feeding trials for each combination of the following food and consumer densities: 5×10^4 , 1×10^5 , 2.5×10^5 , 5×10^5 , 1×10^6 *Monoraphidium*/mL; 1, 5, 25, 125 *Brachionus*/mL. Because it was impossible to perform all experiments on the same day, we tested only one food concentration per day, but tested all consumer concentration levels

on each day. The experimental volume was 50 mL for the 1 *Brachionus*/mL treatment and 8 mL for all other consumer densities. Different volumes were used to allow for sufficient numbers of individuals for radioactivity measurements (at the low *Brachionus* concentration) and to avoid delays due to the transfer of large numbers of individuals (at high concentrations). Prior to the experiments, rotifer cultures were sieved through a 50- μ m mesh to remove the algae and re-suspended in fresh algal solution of the concentration to be tested on that day, allowing animals to adapt to experimental conditions. Depending on the treatment, we pipetted 50, 40, 200, or 1000 adult rotifers under a stereomicroscope into the experimental vessels and subsequently filled these with algal solution to exactly half the experimental volume (25 mL or 4 mL). We then measured the algal concentration again (CASY particle counter), which usually differed slightly from the target concentration. Our accounting for this fact in the data analysis leads to a scattering of algal density data, except for the lowest algal densities where the particle counter was too inaccurate and the exact density was assumed for all parallels. On each day, we also prepared four control treatments that contained 80 rotifers in 4 mL of medium without algae.

Feeding trials were started within 30 min after transferring the rotifers to the experimental vessels by adding 25 mL or 4 mL of radioactively labeled algal solution, respectively. Controls received 4 mL of particle-free filtrate (Whatman Nucleopore, 0.2 μ m, Whatman, Clifton, New Jersey, USA) from the labeled algal solutions to account for non-particulate uptake of radioactivity. Trials lasted 4 min each, which is shorter than *Brachionus*' gut passage time (Starkweather and Gilbert 1977), and were terminated by adding 5 mL of carbonized water for narcotization and, 30 s later, 200 μ l of 37% formaldehyde. Dead rotifers were washed with deionized water on 50- μ m nets, and groups of 30–80 animals per sample were transferred with some water into scintillation vials. We dissolved rotifers with 2 mL of tissue solubilizer, added 3.5 mL of toluene-scintillator, and measured disintegrations per minute (2300 TR Liquid Scintillation Analyzer, Packard Instruments, Downers Grove, Illinois, USA). Five milliliters of labeled algal suspension (five replicates) were filtered, and the filters were solubilized and measured as described. Control radioactivity was subtracted from radioactivity measured in other samples, and individual ingestion and clearance rates were calculated according to Peters (1984).

Statistical analyses

In our analyses of experimentally determined functional response curves, we followed the guidelines of Juliano (2001), the most up-to-date treatment of this issue. Data analyses consisted of three consecutive steps: (1) determine the type of functional response, (2) estimate the parameters of a mechanistic model of

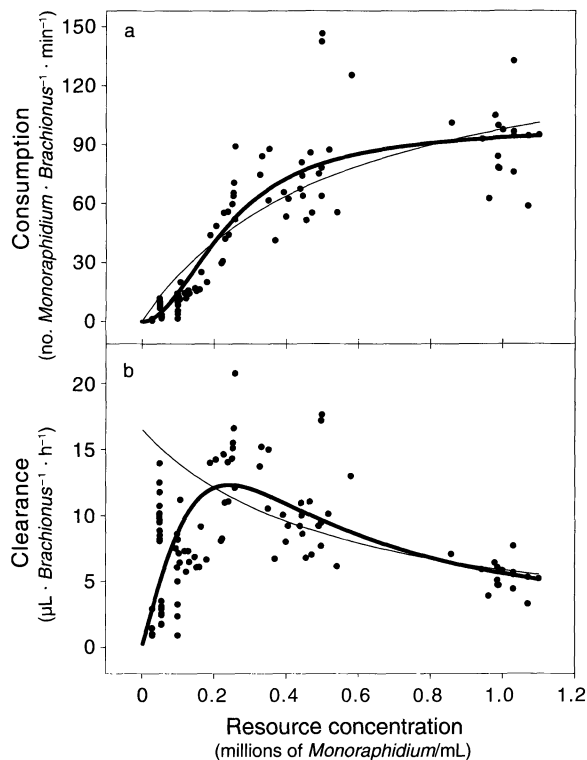


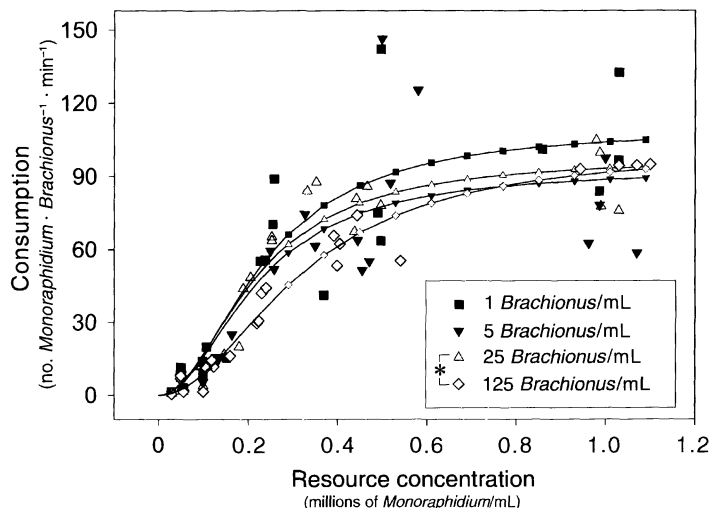
FIG. 1. (a) Consumption and (b) clearance rates of the rotifer *Brachionus calyciflorus* (consumer; all concentrations are plotted) for the unicellular green alga *Monoraphidium minutum* (resource). Thick and thin lines are fitted curves (nonlinear regression) for Holling type 3 and Holling type 2 functional responses, respectively.

functional response, and (3) determine whether parameters describing separate functional response curves at different consumer densities are statistically different. See Appendix A for a detailed description of the statistical analyses associated with these three steps and for information on fitting the ratio-dependent model to our data.

RESULTS

The consumption rate of *Monoraphidium* by *Brachionus* was best described by a sigmoid Holling type 3 functional response (Holling 1959). A logistic regression performed on the standardized proportions of *Monoraphidium* consumed yielded a significantly positive linear term and a significantly negative quadratic term (Appendix B), indicating an inverse parabola, i.e., a curve that increases at the lowest algal densities but decreases at higher algal densities. This means that the effectiveness with which *Monoraphidium* is consumed (or the clearance rate) has a maximum for intermediate algal densities (Fig. 1b). Subsequent analyses revealed that our functional response data are consistent with the Holling type 3 response, where the attack rate, a , varies as a linear function of the resource concentration, R (Eqs. A2 and A3; Appendices A and B). Conse-

FIG. 2. Consumption rates of *B. calyciflorus* (as in Fig. 1a) at four different consumer concentrations (large symbols). Lines with small symbols are fitted curves for Holling type 3 functional responses for each consumer concentration. The asterisk in the key denotes a statistically significant difference between parameters fitted to the respective curves (after Bonferroni correction; see Appendix B).



quently, this functional response was fitted to the experimental data using nonlinear regression and resulted in a much better fit than the alternative Holling type 2 model (Fig. 1). We performed the same statistical analysis on the four subsets of data representing the four different *Brachionus* concentrations at which we ran our experiments. In each of these cases, we found significantly positive linear terms and significantly negative quadratic terms in logistic regression analyses, as well as linear relationships between attack rates and resource concentrations (Appendix B). We were thus able to fit separate Holling type 3 curves for each consumer concentration (Fig. 2).

Because the same model with the same two parameters could be fitted to each functional response curve, testing for statistically significant differences among the parameter values was a straightforward technique to decide whether functional responses were different at the four experimental consumer densities. We found no significant differences among the four values of the parameter “handling time, T_h ” (Appendix B). The second parameter was b , the constant of proportionality of the linear relationship between successful attack rate and resource concentration (Eq. A3; Appendix A). For this parameter, the three pairwise comparisons that included the highest consumer concentration (125 *Brachionus*/mL) resulted in the three lowest P values (Appendix B). However, only the comparison between the 25 /mL and 125 /mL treatment showed a significant difference in b after Bonferroni correction. This can be explained by the comparatively low data scatter in the 25 *Brachionus*/mL treatment (Fig. 2), which allowed parameter estimates with narrow confidence intervals (Appendix B). Although our experiments were very short, resource depletion may still have occurred. We therefore also fitted a type 3 functional response model to the data that accounts for resource depletion (Appendix A). Our general findings were supported by this model as well (Appendix B). In summary, the statistical

tests confirm the impression of only marginal differences among the functional response curves that a visual inspection of the data suggests. We detected partial evidence for consumer-dependent resource uptake if and only if the consumer concentration in the experiments was extremely high.

The ratio-dependent model was inappropriate for our data and provided a worse fit than the classical prey-dependent model (residual sum of squares equalled 115,157 for ratio dependence [Eq. A5; Appendix A]; and 24,161 for prey dependence ([Eq. A3; Appendix A]). Fig. 3 illustrates that the best ratio-dependent fit systematically underestimated resource consumption.

DISCUSSION

Our study showed that the per capita food uptake of the rotifer *B. calyciflorus* depends on the food concentration, but does not depend on the consumers' density within a range of consumer densities typically observed in nature. This result is consistent with the classical concept of resource- (or prey-) dependent consumption, but contradicts the more recently developed concept of consumer (or predator) dependence. In particular, our data showed no support for ratio-dependent consumption, a special case of consumer dependence. Among the few studies that explicitly tested between these two competing theories, our results are the first to support prey dependence.

As a “by-product,” our study suggested a Holling type 3 functional response for *B. calyciflorus*, which is characterized by maximum clearance rates at intermediate food concentrations. Usually, plankton grazers display a type 2 or type 1 response (Rothhaupt 1990, Jeschke et al. 2004), although type 3 responses are not uncommon (Jeschke et al. 2004) and have been reported previously for *B. calyciflorus* (Halbach and Halbach-Keup 1974). Filter feeders usually show type 3 responses when they reduce their filtration rate in times of low food abundance (Jeschke et al. 2004), and we

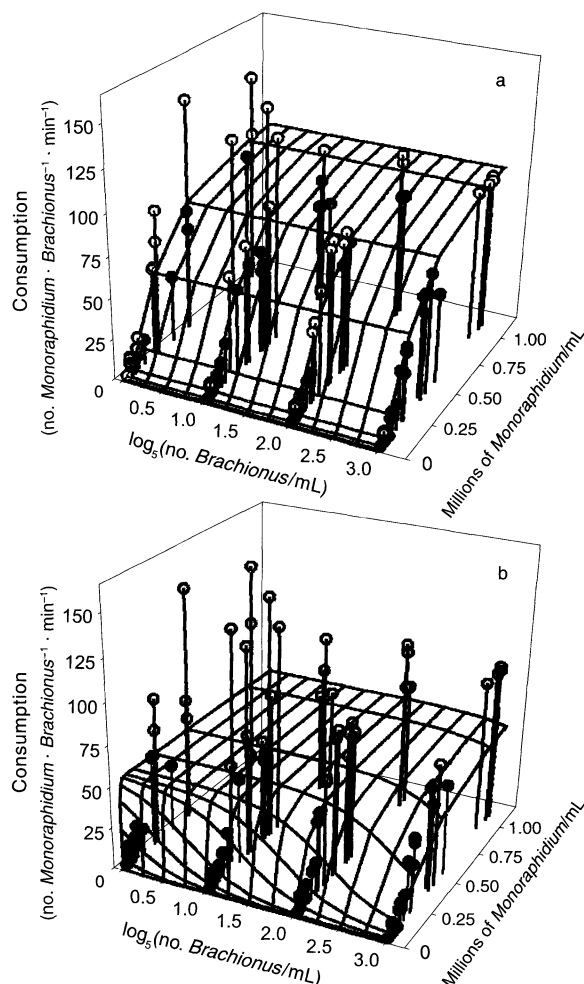


FIG. 3. Comparison of the prey-dependent fit (plane in panel a) with the ratio-dependent fit (plane in panel b) to the data (both Holling type 3). Solid symbols indicate data points beneath the fitted plane, and empty symbols are above the fitted plane; otherwise data are identical in panels a and b.

assume that this was the case in our experiments. However, determining the shape of the functional response was not our central goal, and, therefore, we collected no additional data to explain why clearance rates declined at the lowest algal densities. For our study, it was only important that functional response was uniformly of the same type across all consumer densities.

Consumer-dependent food uptake is conceivable in planktonic consumers, and there are two short-time scale mechanisms that are potentially responsible for its occurrence: (1) Chemicals released by consumers can serve as indicators of crowding and cause the consumers to alter their foraging or feeding behavior (Helgen 1987, Lüring et al. 2003), and (2) increased consumer density can lead to higher encounter probability of consumer individuals with consequences for feeding behavior. Our experiments were probably too short to detect density-dependent effects of the first type. By

minimizing experimental duration, we decided to investigate the more generic effect of direct predator interference. Longer experiments and pre-adaptation phases would have resulted in excessive resource depletion and changes in consumer densities because of reproduction. Consequently, we have no evidence for the first mechanism to be important in our system, but we found evidence from our own cultures suggesting that encounters of *Brachionus* individuals potentially reduce feeding rates through physical interference. Free-swimming *Brachionus* individuals that hit an obstacle (or another *Brachionus* individual) in a petri dish will retract their anterior corona for a few seconds and stop moving their wheel organ, which is used for both food uptake and locomotion (*personal observation*). This proposed mechanism did not, however, lead to significant consumer dependence of the functional response at the four consumer densities we tested. At the highest rotifer density (125 rotifers/mL), ingestion rates (Fig. 2) and the parameter b (the constant of proportionality between attack rate and resource concentration) tended to be lowest, but there was no consistent pattern of significant differences among the parameters describing the fitted functional response curves (Appendix B). This may indicate that 125 *Brachionus*/mL is a consumer density at which physical interference between consumers begins to become important. The fact that differences in handling time, T_h , were never even marginally significant supports our assumption about the potential mechanism of interference in our system. Corona retraction is supposed to effectively reduce the attack rate of the rotifers, but not to preclude them from processing already ingested food.

We performed our experiments at rather high rotifer densities compared with densities observed in the field, where total rotifer abundance is typically below 1 rotifer/mL (Yoshida et al. 2000, Wetzel 2001). Seasonal peaks of extremely high rotifer abundance can occur in highly productive lakes. For instance, Lampert and Rothhaupt (1991) reported 47.3 rotifers/mL from a shallow, brackish water lake; Jürgens et al. (1999) observed 5.8 *B. calyciflorus*/mL in a shallow, hypertrophic lake; and Snell and Serra (1998) reported ~9 *B. rotundiformis*/mL in a brackish water pond. These extreme values are still considerably lower than our maximum experimental density of 125 *B. calyciflorus*/mL, and, therefore, we conclude that food uptake by grazing rotifers is unlikely to be consumer dependent in the wild. In aquaculture facilities, where *Brachionus* spp. are being mass-cultured as live food for larval fish, densities can reach $>10^5$ *Brachionus*/mL (Yoshimura et al. 2003). Our results do not permit conclusions about such densely packed artificial cultures, but it seems likely that physical interference can lead to consumer dependence in them.

The radiotracer method has been widely used to measure the food uptake of microzooplankton (Schindler 1968, Starkweather and Gilbert 1977, Rothhaupt 1990),

although we know of no previous studies that used this technique to systematically measure over a wide range of consumer densities. Walz and Gschloessl (1988) determined the uptake of radiolabeled algal food at two concentrations of *Brachionus angularis* and detected no significant differences between the filtration rates. Since rotifer densities differed in that study (Walz and Gschloessl 1988) only by a factor of two (28 and 56 rotifers/mL), it hardly constitutes a test of resource vs. consumer dependence, but is in clear agreement with our results demonstrating prey dependence over more than two orders of magnitude of consumer densities.

There are several experimental studies that have found, contrary to our results, uptake or capture rates of prey by zooplankton to depend on the consumers' density (Salt 1974, Hayward and Gallup 1976, Helgen 1987, Arditi et al. 1991, Arditi and Saiah 1992, Jost and Ellner 2000, Hansson et al. 2001, Lüring et al. 2003). As a common weakness, all these studies share an indirect or non-instantaneous approach to the problem. Consumer dependence is either inferred indirectly from observed plankton population dynamics (Arditi et al. 1991, Arditi and Saiah 1992, Jost and Ellner 2000) or the duration of the experiments was sufficiently long for prey depletion to occur (Salt 1974, Hayward and Gallup 1976, Helgen 1987, Hansson et al. 2001, Lüring et al. 2003). Both techniques introduce sources of error that the direct method we used (short-term experimentation with radiolabeled food) avoids. It is interesting to note that in many of these studies, mechanisms other than direct physical interference in a homogeneous environment appear to be responsible for consumer dependence. Helgen (1987) and Lüring et al. (2003) found that medium that was conditioned by high numbers of grazing cladocerans led to a reduction in grazing rates, which strongly suggests chemical interactions. Jost and Ellner (2000) suggest predator aggregation due to local prey depletion and, in what was a first definite experimental test of the ratio-dependence hypothesis, Arditi et al. (1991) and Arditi and Saiah (1992) were able to demonstrate ratio dependence for two cladoceran species that showed a spatially heterogeneous behavior, but were unable to do so for two other cladocerans with homogeneous spatial behavior (Abrams 1994, Holmgren and Lundberg 1996). Therefore, we see our contribution not necessarily as a contradiction to these previous studies, but as a treatment of the most general case, assuming that the plankton organisms' behavior can be approximated to that of randomly moving particles. Finally, we suggest that the scarcity of support for prey dependence in the literature could be the result of a reporting bias due to the fact that some ecologists judge evidence for prey dependence as an unimportant, a standard, or a "negative" result (the latter referring to the "post-ratio-dependent era" after the year 1989).

We conclude that predator dependence due to physical interference among rotifers in homogeneous plank-

ton communities is unlikely to occur in the field. Hence, assuming prey dependence and not predator dependence (or ratio dependence) should be the norm in dynamic mathematical models describing these and similar communities.

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APPENDIX A

A description of statistical methods is available in ESA's Electronic Data Archive: *Ecological Archives* E086-158-A1.

APPENDIX B

Statistical tables for analyses discussed in the text are available in ESA's Electronic Data Archive: *Ecological Archives* E086-158-A2.