



Promoting the Science of Ecology

---

Empirical Evidence of the Role of Heterogeneity in Ratio-Dependent Consumption

Author(s): Roger Arditi and Henni Saiah

Source: *Ecology*, Vol. 73, No. 5 (Oct., 1992), pp. 1544-1551

Published by: Ecological Society of America

Stable URL: <http://www.jstor.org/stable/1940007>

Accessed: 18/09/2009 10:35

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=esa>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

## EMPIRICAL EVIDENCE OF THE ROLE OF HETEROGENEITY IN RATIO-DEPENDENT CONSUMPTION<sup>1</sup>

ROGER ARDITI AND HENNI SAÏAH

*Institute of Zoology and Animal Ecology, University of Lausanne, CH-1015 Lausanne, Switzerland*

**Abstract.** Classical models describing the number of prey consumed by predators rest on an analogy with the law of mass action and, consequently, the functional response of predators depends only on the density of prey. An alternative model is that the functional response depends on the ratio of prey and predator densities. We hypothesize that the applicability of one or the other model depends on the degree of heterogeneity of predators and prey in space, the prey-dependent model being appropriate in homogeneous situations while the ratio-dependent model is appropriate in heterogeneous situations. We have designed experiments to test this hypothesis, using cladocerans filter-feeding on algae. The design is such that the two types of dependence can be discriminated by observation of equilibrium patterns. *Daphnia magna* and *Simocephalus vetulus*, the two cladoceran species tested, differ in their spatial distributions. *Daphnia* has homogeneous distribution whereas *Simocephalus* has heterogeneous distribution. Experimental results support the hypothesis: *D. magna* follows the prey-dependent model and *S. vetulus* follows the ratio-dependent model. By artificially modifying the environment of the two species, we forced *D. magna* to a heterogeneous distribution and *S. vetulus* to a homogeneous distribution. As a consequence, each species changed its dependence, further confirming our hypothesis.

**Key words:** cladocerans; consumption rate; *Daphnia*; density dependence; functional response; plankton grazing; population dynamics; predator–prey theory; ratio dependence; *Simocephalus*; spatial heterogeneity.

### INTRODUCTION

Ratio dependence refers to the functional form of the *trophic function* of predators,  $g$ , i.e., the amount of food eaten per predator per unit time. This function  $g$  (also known as the *functional response*) is best defined in the context of the standard predator–prey model

$$\frac{dN}{dt} = f(N)N - g(\cdot)P \quad (1a)$$

$$\frac{dP}{dt} = eg(\cdot)P - \mu P, \quad (1b)$$

where  $f$  is the production rate,  $e$  the conversion efficiency of predators, and  $\mu$  the predator death rate.

The ratio-dependent theory asserts that  $g$  depends on the prey/predator ratio:  $g = g(N/P)$ , while the usual assumption following Lotka and Volterra is that  $g$  only depends on prey abundance:  $g = g(N)$ . Naturally, it is quite possible that the functional response depends separately on both variables  $N$  and  $P$  [ $g = g(N, P)$ ], but it is useful to have a simpler expression and it is important to know which of the two simple forms better describes real situations.

The traditional prey-dependent model is derived from the original Lotka–Volterra model where  $g(N) = aN$ , which is nothing more than the law of mass action of chemistry: the predator–prey interaction term assumes that predator and prey individuals randomly encounter each other in the same way that molecules interact in a chemical solution. Arditi and Ginzburg (1989) argue that an ecological system can only be appropriately described by such a model if it is sufficiently homogeneous, both with respect to the physical environment and with respect to individual spatial behavior. Bacteria feeding in a stirred chemostat are a good example. In heterogeneous situations, it is suggested that  $g = g(N/P)$  should be a more reasonable model. This form reflects the fact that, in some sense, predators must “share” the available prey. Further theoretical considerations about the ratio-dependent version of the model (Eqs. 1), or about other ratio-dependent models have been given on several occasions (Getz 1984, Ginzburg 1986, Akçakaya et al. 1988, Arditi and Ginzburg 1989, Arditi and Akçakaya 1990, Berryman 1990, Arditi and Berryman 1991, Arditi et al. 1991a, Hanski 1991, Akçakaya 1992).

Here, we address the problem of discriminating between the two models using empirical evidence. The question is twofold. First, is it possible to identify the

<sup>1</sup> For reprints of this Special Feature, see footnote 1, p. 1529.

underlying trophic function from observed patterns of population dynamics or statics? Second, is the occurrence of ratio dependence related to heterogeneity and the occurrence of prey dependence related to homogeneity?

Empirical evidence can be classified into three categories: (1) Direct measurements of the functional response  $g(N,P)$ , i.e., counts of prey eaten in a given time by a given number of predators when offered a given number of prey. Such data come mostly from laboratory experiments with insects. (2) Cases where the number of prey eaten cannot be observed directly, but where some assessment of the functional form of  $g$  can be inferred from comparisons made between distinct but similar ecosystems. (3) Experiments designed in such a way that the two models can be discriminated on the basis of population statics, i.e., on the basis of counts of prey and predator numbers in a given ecosystem. Thus, the two last categories permit an indirect statement about the function  $g$ , based on properties of the entire dynamical system (Eqs. 1).

In this paper, we first review published experimental results and observational data (categories 1 and 2) that allow discrimination between the two opposing models. Then, we report results from new laboratory experiments devised to investigate the ratio-dependent relationship (category 3).

AVAILABLE EVIDENCE

*Direct observations of the functional response*

At first, it might seem a simple thing to assess ratio dependence by direct measurements of the functional response: i.e., choose various numbers of prey and predators in fixed proportions and count the number of prey eaten in a given length of time. However, several difficulties make this procedure objectionable, if not worthless.

The first difficulty arises due to prey depletion; i.e., when predators consume prey, prey density decreases from a value  $N$  to a value  $N - \Delta N$ . Thus, it is not possible to observe directly the quantity  $g(N,P)$  which is an instantaneous rate defined for a fixed value of  $N$ . Instead, what can be measured is some integrated value  $G$  over a finite period of time  $T$  and over the finite interval of prey densities  $[N - \Delta N, N]$ .  $G$  results from the integration of Eq. 1a without prey production, i.e.,

$$\frac{dN}{dt} = -g(N,P)P, \tag{2}$$

and, by definition,  $G(N,P,T)$  is defined as

$$G(N,P,T) = \frac{\Delta N}{PT}, \tag{3}$$

where  $\Delta N$  is given by the following equation, obtained

by integration of Eq. 2:

$$\int_{N-\Delta N}^N \frac{dN}{g(N,P)} = PT. \tag{4}$$

Thus, whether  $g = g(N)$  or  $g = g(N/P)$ , the function  $G$  will not have the same type of dependence as  $g$ . It will always have separate influences of  $N$  and  $P$ ; in particular, even if  $g$  is not  $P$ -dependent, the very process of prey reduction will induce  $P$ -dependence into the integrated response  $G$ .

Reconstructing the instantaneous response  $g$  from the observation of  $G$  is only possible if an explicit mathematical model is available for  $g(\cdot)$ . One versatile model can be obtained with a modification of the standard Michaelis-Menten-Holling "disk equation":

$$g(N,P) = \frac{\alpha NP^{-m}}{1 + \alpha t_h NP^{-m}}, \tag{5}$$

where  $t_h$  is the handling time and  $\alpha$  is related to the efficiency of searching (Arditi and Akçakaya 1990).

This model, where  $g = g(N/P^m)$ , is a generalization that includes as special cases the two opposed types of dependence. For  $m = 0$ , it reduces to the traditional prey-dependent functional response and, for  $m = 1$ , it becomes ratio dependent. Thus, the parameter  $m$  can be interpreted as a quantification of  $P$  dependence between the two extreme cases.

When the model (Eq. 5) is introduced into Eq. 4, the expression for  $\Delta N$  is given by the following implicit equation

$$\Delta N = N[1 - \exp(-\alpha P^{1-m}T + \alpha P^{-m}t_h\Delta N)] \tag{6}$$

which, with Eq. 3, makes for  $G$  a model with the three parameters  $\alpha$ ,  $t_h$ , and  $m$ . If a sufficient number of observations are available, for several combinations of values of  $N$  and  $P$ , these parameters can be identified by one of several methods, for example by least-squares nonlinear regression.

An analysis of 15 data sets from the literature (Arditi and Akçakaya 1990) has revealed that the parameter  $m$  was always significantly different from zero. In 12 out of the 15 cases, it was not significantly different from one, i.e., the ratio-dependent functional response could not be rejected. In 3 cases,  $m$  had some intermediate value (between 0.3 and 0.6). It should be noted that, in the case of parasitoids, Eq. 6 must be modified to the following expression because attacked hosts remain available for further attack:

$$\Delta N = N \left[ 1 - \exp \left( \frac{-\alpha P^{1-m}T}{1 + \alpha P^{-m}t_h N} \right) \right] \tag{7}$$

In sum, ratio dependence seems to occur quite fre-

quently in simple laboratory experiments. However, the question arises whether these experiments are typical of natural relationships. The main objection (Arditi and Ginzburg 1989) is that, in the laboratory, the rate that is measured, occurs on the behavioral time scale; that is, it is a "microscopic" observation. However, as shown by Eqs. 1, function  $g$  should be considered on the time scale of population dynamics (i.e., prey mortality and predator reproduction). This would require much longer experiments, and is quite impracticable. For this reason, we hold that more convincing evidence about the functional form of  $g$  should come from "macroscopic" properties of the complete dynamical system (Eqs. 1).

#### *Cross-ecosystem comparisons*

Setting Eqs. 1 to zero gives the equilibrium values of prey and predator populations. In particular, Eq. 1b gives very different results with prey-dependent and with ratio-dependent trophic functions  $g$ . It is easy to see that, if  $g = g(N)$ , zeroing Eq. 1b gives a unique value  $N^*$ , irrespective of  $P$ . Thus, in the prey-dependent model, the prey equilibrium is set entirely by predator characters. It does not depend in any way on prey production. On the contrary, in the ratio-dependent model, Eq. 1b solves for a critical ratio  $N^*/P^*$ . Eq. 1a then sets the absolute values of both equilibria.

The same kind of analysis can be applied to the generalization of the model (Eqs. 1) to food chains of arbitrary length. Briefly, the ratio-dependent model predicts that, if primary productivity increases, the abundance of every trophic level will increase. On the other hand, the traditional prey-dependent model forms the basis of the well-known HSS hypothesis ( Hairston et al. 1960). This theory asserts that, in food chains with an odd number of trophic levels, producers would increase, whereas in even-length chains, they would remain constant or decrease. Conflicting predictions are also made at the upper levels. The ratio-dependent model predicts correlated, proportional increases of all prey-predator pairs, while the prey-dependent model predicts uncorrelated or negatively correlated variations of such pairs (Arditi and Ginzburg 1989, Arditi et al. 1991a, Ginzburg and Akçakaya 1992).

Testing the above predictions could be done by manipulating the primary productivity of whole ecosystems. It can also be done indirectly, by comparing similar ecosystems of different productivities. For example, lakes can be ranked according to the input of phosphorus, the most common limiting nutrient to algal production. Data show that, across a gradient of increasing phosphorus loadings, the standing stocks of phytoplankton and of *Daphnia*, its main grazer, are positively correlated. This result is in harmony with the predictions of the ratio-dependent model (Arditi

et al. 1991a). Additional analyses of aquatic systems, at the producer-herbivore levels as well as at higher trophic levels, give similar results (Ginzburg and Akçakaya 1992). A number of terrestrial studies have also shown correlated, increasing abundances of all trophic levels with primary production (Ricklefs 1979: 623, Pimm 1982: 111, McNaughton et al. 1989, Arditi et al. 1991a).

#### PURPOSELY DESIGNED EXPERIMENTS

##### *Experimental rationale*

We have designed experiments to test directly the hypotheses that the prey-dependent model better describes predator-prey dynamics in homogeneous systems (comparable to agitated solutions of molecules), whereas more heterogeneous situations should be better described by the ratio-dependent model. The basic experimental design is documented in Arditi et al. (1991b). Filter-feeding cladocerans are reared in a flow-through system where water containing food particles is pumped into serially arranged containers from which consumers cannot escape (Fig. 1). Starting with an inoculum in each container, the cladoceran populations are allowed to increase or decrease until equilibrium is reached.

This design permits discrimination of the two forms of functional response by observing the patterns of equilibria of consumer populations only. The prey-dependent hypothesis predicts that the first container should stabilize at some population  $P^*$  and that all subsequent containers should become extinct:

$$\text{Pattern } g(N): P^*, 0, 0, 0, \dots$$

This prediction is due to the fact that the prey equilibrium is set by the predator equation (Eq. 1b) only and does not depend on prey "production" (i.e., inflow rate and concentration). Once prey numbers have reached this critical value in the first container, the food concentration flowing into the following containers is too low to sustain a consumer population.

The ratio-dependent hypothesis predicts a very different pattern. Consumer equilibria decline in a geometrical sequence because the predator equation (Eq. 1b) now sets the equilibrium ratio to a constant value:

$$\text{Pattern } g(N/P): P^*, bP^*, b^2P^*, b^3P^*, \dots \\ (\text{where } b < 1)$$

The calculations leading to these predictions are straightforward and can be found in Arditi et al. (1991b).

##### *Methods*

Each experimental cascade consisted of five polyethylene containers (Fig. 1), holding 230 mL of water each, with a wall and bottom surface area of 155 cm<sup>2</sup>.

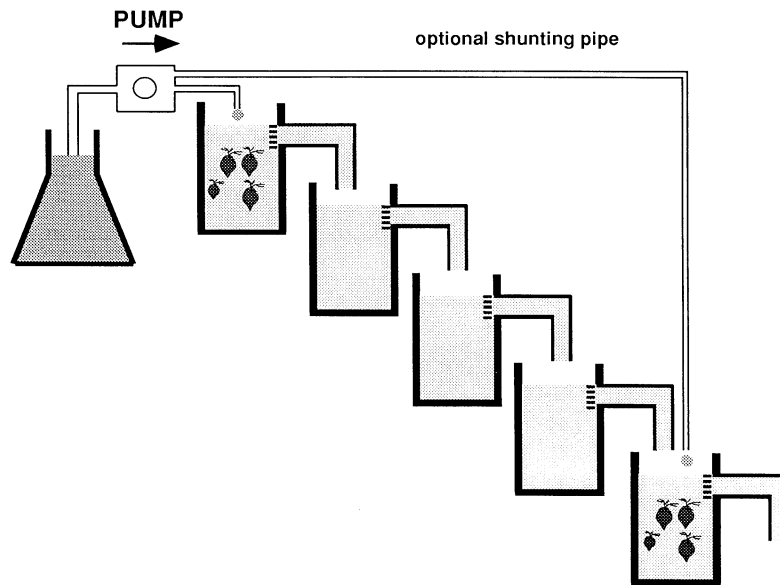


FIG. 1. General experimental design of the cascade of five containers. Algae were pumped at constant flow from a stirred stock tank into the cascade. Starting with an inoculum of cladocerans in each container, population equilibria were reached after a few weeks. Filters prevented the passage of newborn cladocerans through the cascade.

Filters of 300- $\mu\text{m}$  mesh size prevented the passage of newborn cladocerans along the cascade. The food consisted of live *Chlorella vulgaris*. The algal population was stored in a tank where it was constantly stirred. From there, a peristaltic pump introduced a flow of 54.46 mL/h into the experimental cascade. Plain water, at a flow of 201.85 mL/h, was also pumped simultaneously in order to dilute the algae. Two different concentrations were used for the algal supply: 22.4 cells/mL and 146.8 cells/mL. The "low food" cascades received therefore 1222 cells/h and the "high food" ones 7993 cells/h. The water temperature was  $21 \pm 1^\circ\text{C}$ .

We used two different species of cladocerans: *Daphnia magna* Straus and *Simocephalus vetulus* (Müller). *Daphnia* swims constantly and is more or less homogeneously distributed in space. *Simocephalus*, on the other hand, has a special gland on the side of the head for attaching to substrates, and in the experiments it generally attached to the walls of the containers; in nature, it rests on leaves of macrophytes. We expected that *Daphnia* would follow the prey-dependent model while *Simocephalus* would follow the ratio-dependent model. Single clones were used for each species. They reproduced parthenogenetically for the whole duration of the experiments.

Each species was studied in plain containers as well as in modified ones. The basic idea was to force each species to follow the spatial distribution of the other. With *Daphnia*, we added in each container a 98-mL cylinder made with 300- $\mu\text{m}$  mesh polyester fabric,

making the center of the container inaccessible; the consumers were forced to swim and feed along the walls and the bottom of the containers. With *Simocephalus*, we modified the spatial environment by offering a large number of additional resting places within each container. These places were made of several discs of thick polyester fabric, allowing free passage for swimming individuals and making up a total available surface area of 120  $\text{cm}^2$ . Thus, *Daphnia* was forced to a heterogeneous distribution while *Simocephalus* was allowed to occupy a more homogeneous distribution. We predicted that these modifications would cause populations of each species to follow the opposing model with respect to the unmodified situation. The modified environment for *Daphnia* was not run at high food conditions. Each experimental situation was run in two replicates. Thus, a total of 14 cascades were analyzed.

Once a week, each population was censused exhaustively. A Pasteur pipette was used to catch the individuals and transfer them to a temporary container. In addition, the size structure (i.e., the age structure) of each population was estimated with the help of filters. *Daphnia* was classified into three size classes (average sizes 0.903, 1.907, and 3.07 mm) and *Simocephalus* into four classes (0.806, 1.066, 1.378, and 1.682 mm). The body lengths were determined by measuring ( $\pm 0.001$  mm) 40 individuals of each class from the top of the head to the base of the spine (*Daphnia*) or to the bottom of the body (*Simocephalus*). Based on the estimates of size structure, the population biomass could

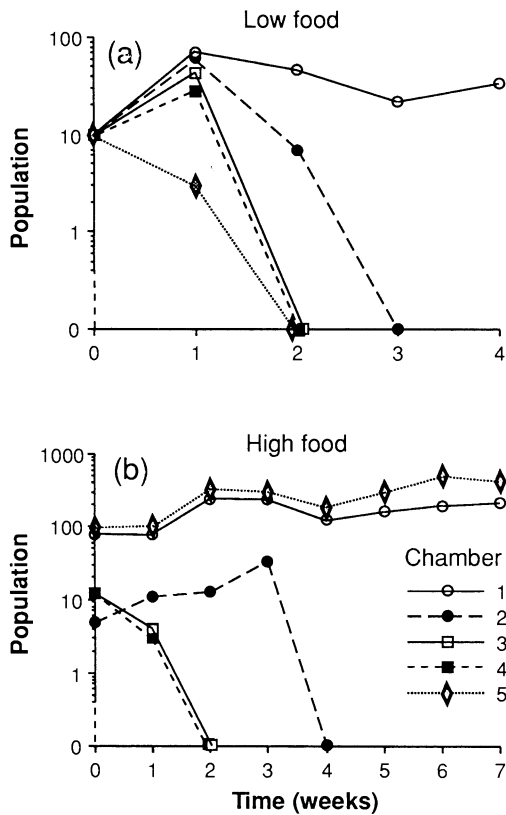


FIG. 2. Population dynamics through time (log scale) of *Daphnia magna* in the five containers of the cascade, under (a) low-food, (b) high-food conditions. With the exception of the first chamber, all populations declined, with populations going extinct sooner in the more distant chambers. In the high-food condition (b), the last chamber was directly fed like the first one and sustained approximately the same stable population. These results are consistent with the prey-dependent prediction.

be calculated, using the following allometric equations (Dumont et al. 1975):

for *D. magna*:

$$W = 1.89 \times 10^{-6} L^{2.25}$$

(length  $L$  in  $\mu\text{m}$  and mass  $W$  in  $\mu\text{g}$ )

for *S. vetulus*:

$$W = 7.43 L^{3.28} \quad (L \text{ in mm and } W \text{ in } \mu\text{g})$$

In order to have a constant consumer mortality  $\mu$ , as required by the model (Eqs. 1), a uniform harvesting rate of 10% was applied in all containers. In those containers where extinctions occurred (*Daphnia* experiments), *Daphnia* populations were restarted with 4–5 individuals and harvesting was discontinued. However, these populations always became extinct

again, confirming that the zero equilibrium was a stable attractor.

The experiments were run until reasonably stationary levels were reached in each container. Stationarity was checked in terms of number of individuals, and in terms of biomass and size structure. The "equilibrium" values were estimated as the average of the last 3 wk in the two replicates.

In some of the cascades (essentially, those at high feeding conditions), algae were also directly introduced into the fifth container, at the same flow rate as into the first one (see Fig. 1). This modification was done in order to determine if upstream populations had some chemical influence downstream. In the absence of such influence, one should expect that the directly fed fifth container should sustain a population identical to the first container.

### Results

Equilibrium conditions were obtained relatively quickly, in 4–7 wk, and in all experiments the dynamics of the two replicates were very similar. Surprisingly, we did not observe the population oscillations common in many laboratory studies of cladocerans.

Under the two feeding conditions, *Daphnia* maintained a stable population in the first container only (Fig. 2). In the other containers, populations became progressively extinct starting with the last and ending with the second. Under the high-food condition, the fifth container was directly fed at the same rate as the first. In this case, the last container reached a population slightly higher than the first (Fig. 2b). This was probably due to some production of algae and microorganisms in the previous compartments, increasing the total food in the final container.

*Simocephalus* presented completely different dynamics and patterns of equilibria, reaching stable populations in all chambers of the cascade (Fig. 3). At both feeding levels, this equilibrium pattern followed approximately a geometric decrease from the first to the last chambers. However, the last container exhibited a significant upward deviation which may be due to the reasons previously suggested for *Daphnia*.

Populations reached stable equilibria in terms of biomass as well as the numbers of individuals. In addition, the size structure attained a stationary state. For illustration, Fig. 4 depicts the dynamics of the size classes of the *Simocephalus* experiment under the low-food condition.

The results are consistent with the expectation that different spatial behaviors should lead to different mathematical models for the trophic function, heterogeneous distributions being associated with ratio dependence and homogeneous distributions with prey dependence. This was corroborated by the results of

the experiments in which the spatial distribution was artificially modified (Figs. 5 and 6).

With *Daphnia*, the addition of an inaccessible cylinder in the center of the containers (43% of the water volume) induced spatial heterogeneity by creating a refuge for the prey. This modification changed the pattern of population equilibria along the cascade (Fig. 5). As with *Simocephalus* (Fig. 3), we obtained stable pop-

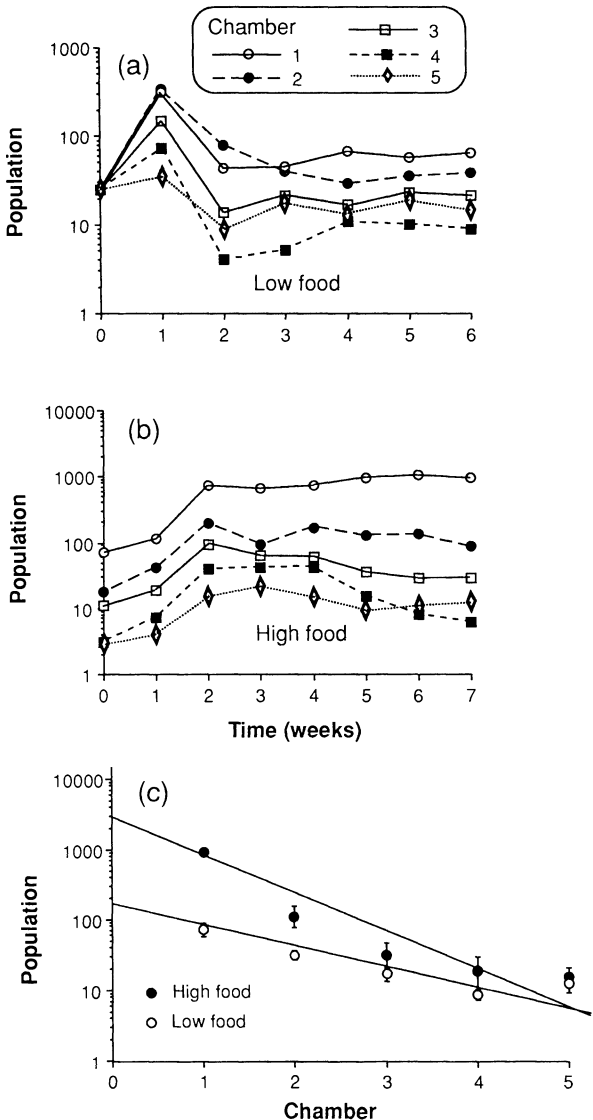


FIG. 3. Population dynamics through time (log scale) of *Simocephalus vetulus* in the five containers of the cascade, under (a) low-food, (b) high-food conditions. (c) Population equilibria (log scale) in each chamber under the two food conditions. Each point is the average of six values (last 3 wk of each of two replicates). These equilibria follow approximately a geometric decline, consistent with the ratio-dependent hypothesis.

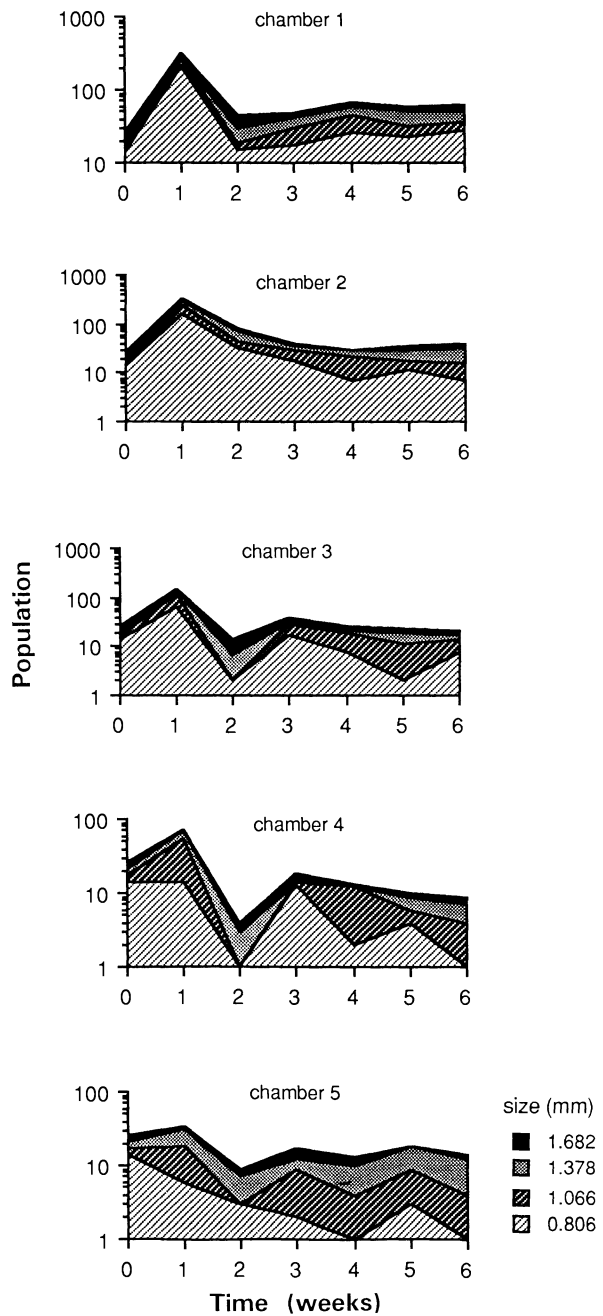


FIG. 4. Size-structured population dynamics of *Simocephalus vetulus* (under low-food condition) in each container (four size classes: 0.806, 1.066, 1.378, and 1.682 mm). The stability of the populations along the cascade seems to decrease from the first chamber to the last.

ulations in all chambers with an approximate geometrical decrease. The low population in the first container may be due to the fact that the inflow of algae dropped from a lower height than in the following ones, badly homogenizing the distribution of algae.

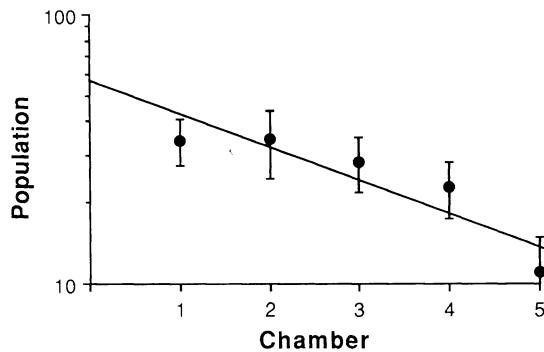


FIG. 5. Equilibrium population densities (log scale) in modified setup for *D. magna* (under high-food condition). Addition of a cylinder in the center of each container (permeable to the algae but not the *Daphnia*) changes the pattern of equilibria of *Daphnia* to that of *Simocephalus*. Each point is the average of six values (last 3 wk of each of two replicates).

In the experiment with *Simocephalus*, spatial homogeneity was increased by adding more resting places. This gave rise to the same equilibrium pattern as in *Daphnia* (Fig. 6), with a nonzero equilibrium in the first container only. In the second chamber, the small population ( $16 \pm 8$  individuals) that subsisted after 7 wk later became extinct.

Table 1 summarizes the equilibrium results of all experiments.

DISCUSSION

The traditional model for describing the prey-predator interaction relies on the law of mass action, treating interacting individuals as randomly moving interacting molecules. It is a simple mechanistic and behavioral model with much intuitive appeal. However, this model has a number of consequences that are clearly counterintuitive. Most striking is the assertion that, in predator-prey systems, the predator biomass only will benefit from increased prey production. In longer food chains, the last, topmost trophic level

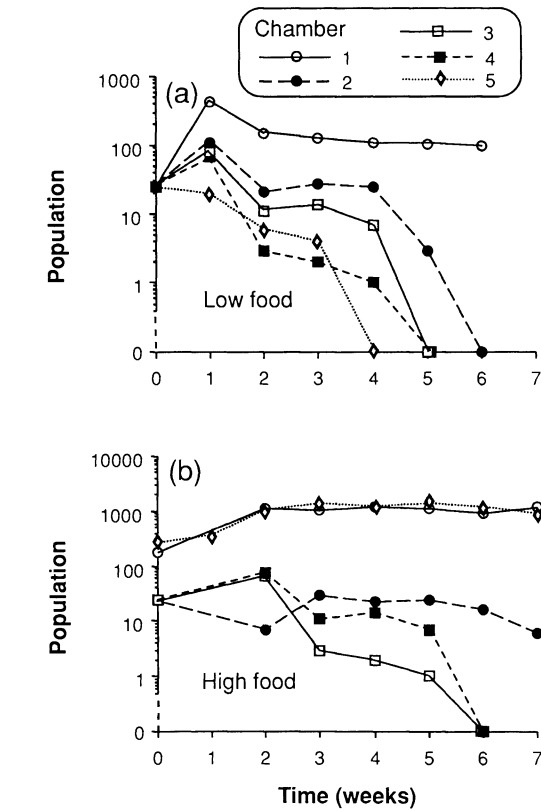


FIG. 6. Population dynamics through time (log scale) of modified setup for *S. vetulus*, under (a) low-food, (b) high-food conditions. Addition of more resting places in the five containers changed the pattern of equilibria of *Simocephalus* to that of *Daphnia*. Each point is the average of six values (last 3 wk of each of two replicates).

responds proportionately to primary production. Depending on the chain length, the biomass of lower levels can either decrease or weakly increase with increased primary production. The ratio-dependent model, on the contrary, predicts that all trophic levels should ben-

TABLE 1. Population equilibria reached in each container in each experiment. Each value is the average of six measures (last 3 wk of each of two replicates).

| Experiment                                      | Container  |          |         |         |            |
|---|------------|----------|---------|---------|------------|
|   | 1          | 2        | 3       | 4       | 5          |
| <i>Daphnia</i> , low food                       | 31 ± 9     | 0        | 0       | 0       | 0          |
| <i>Daphnia</i> , high food                      | 195 ± 38   | 0        | 0       | 0       | 264 ± 54   |
| <i>Simocephalus</i> , low food                  | 75 ± 16    | 32 ± 5   | 18 ± 4  | 9 ± 1   | 13 ± 4     |
| <i>Simocephalus</i> , high food                 | 951 ± 110  | 115 ± 38 | 32 ± 15 | 19 ± 12 | 16 ± 6     |
| <i>Daphnia</i> , with cylinders*                | 34 ± 7     | 34 ± 10  | 28 ± 7  | 23 ± 5  | 11 ± 4     |
| <i>Simocephalus</i> , resting places, low food  | 97 ± 25    | 0        | 0       | 0       | 0          |
| <i>Simocephalus</i> , resting places, high food | 1079 ± 124 | 16 ± 8   | 0       | 0       | 1123 ± 130 |

\* Cylinders were permeable to the algae but not the *Daphnia*, restricting these consumers to the peripheral portions of the containers.



efit from such increase of primary production. Indirect evidence, obtained by comparing similar ecosystems of different productivities, suggests that the predictions of the ratio-dependent theory are in closer agreement with the observations.

The ratio-dependent theory has no simple, mechanistic foundation comparable to the law of mass action. We have suggested that the reasons natural systems seem to respond in a ratio-dependent manner must lie in the factors that make real ecosystems impossible to reduce to chemical solutions—most of all, spatial and temporal heterogeneities. The experiments we have reported here were designed to test this suggestion. Results fully support the assertion that homogeneous conditions lead to prey dependence while heterogeneous conditions lead to ratio dependence. Different spatial behaviors of *Daphnia magna* (homogeneous) and of *Simocephalus vetulus* (heterogeneous) lead to the two different types of dependence. With artificial manipulation of the environment, we have been able to force *D. magna* to a heterogeneous distribution and *S. vetulus* to a homogeneous one. Each species then followed the dynamics of the other species.

Since cladoceran mortality was maintained constant, we can also rule out density-dependent mortality in the predator equation as a possible explanation of the two contrasting equilibrium patterns. This mechanism was suggested by Gatto (1991) to explain the pattern of positive correlations between algae and zooplankton biomasses among lakes of differing productivities.

Conceptually, there is no need to restrict possible functional responses to either prey dependence or strict ratio dependence. As explained earlier, an "intermediate" model of type  $g = g(N/P^m)$  can be constructed. It includes prey dependence and ratio dependence as special cases ( $m = 0$  and  $m = 1$ , respectively). However, as we have shown, experimental evidence does not indicate that such intermediate situations occur frequently. In our experimental setup, intermediate values of  $m$  would lead to nonlinear relations in the graphs of log equilibria against chamber numbers (e.g., Figs. 3 or 5). While these figures suggest some curvilinearity (of opposed convexities), in general the relations are well fit by linear regression. Besides, we have suggested some reasons for the deviations of the first and last containers.

In summary, our experimental results are in harmony with the theoretical assertion that heterogeneity generates ratio dependence. In addition, field data show that in natural ecosystems (which are intrinsically heterogeneous), patterns of population equilibria also agree with ratio-dependent consumption laws.

#### ACKNOWLEDGMENTS

We are indebted to Christian Koenig and Patrick Moratal for technical help. The ratio-dependent theory and the ideas underlying the experimental setups have been discussed with many people. We thank particularly Alan Berryman, Pamela Matson, and Gary Mittelbach for comments on an earlier version of the present paper.

#### LITERATURE CITED

- Akçakaya, H. R. 1992. Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. *Ecological Monographs* **62**:119–142.
- Akçakaya, H. R., L. R. Ginzburg, D. Slice, and L. B. Slobodkin. 1988. The theory of population dynamics: II. Physiological delays. *Bulletin of Mathematical Biology* **50**:503–515.
- Arditi, R., and H. R. Akçakaya. 1990. Underestimation of mutual interference of predators. *Oecologia (Berlin)* **83**:358–361.
- Arditi, R., and A. A. Berryman. 1991. The biological control paradox. *Trends in Ecology and Evolution* **6**:32.
- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology* **139**:311–326.
- Arditi, R., L. R. Ginzburg, and H. R. Akçakaya. 1991a. Variation in plankton densities among lakes: a case for ratio-dependent predation models. *American Naturalist* **138**:1287–1296.
- Arditi, R., N. Perrin, and H. Saïah. 1991b. Functional responses and heterogeneities: an experimental test with cladocerans. *Oikos* **60**:69–75.
- Berryman, A. A. 1990. Population analysis system: POPSYS Series 2, two-species analysis. *Ecological Systems Analysis*, Pullman, Washington, USA.
- Dumont, J. J., I. van de Velde, and S. Dumont. 1975. Length-dry weight relationships and growth of Cladocera from the River Thames, Reading. *Oecologia (Berlin)* **19**:75–97.
- Gatto, M. 1991. Some remarks on models of plankton densities in lakes. *American Naturalist* **137**:264–267.
- Getz, W. M. 1984. Population dynamics: a *per capita* resource approach. *Journal of Theoretical Biology* **108**:623–643.
- Ginzburg, L. R. 1986. The theory of population dynamics: I. Back to first principles. *Journal of Theoretical Biology* **122**:385–399.
- Ginzburg, L. R., and H. R. Akçakaya. 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. *Ecology* **73**:1536–1543.
- Hairton, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control and competition. *American Naturalist* **94**:421–425.
- Hanski, I. 1991. The functional response of predators: worries about scale. *Trends in Ecology and Evolution* **6**:141–142.
- McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* **341**:101–105.
- Pimm, S. L. 1982. *Food webs*. Chapman and Hall, London, England.
- Ricklefs, R. E. 1979. *Ecology*. Second edition. Chiron, New York, New York, USA.