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DAPHNIA-PHYTOPLANKTON INTERACTIONS IN LAKES: IS THERE A NEED FOR RATIO-DEPENDENT CONSUMER-RESOURCE MODELS?

Consumer-resource models of the Lotka-Volterra type have been a standard tool for population theoreticians, and much of current population and community theory has been derived from population models with Lotka-Volterra type consumer-resource dynamics (see reviews in Rosenzweig 1977; Taylor 1984; Yodzis 1989). A fundamental assumption of these models is the exclusive dependence of the consumer's functional response on resource density and its independence of consumer density. The generality of this assumption has been questioned by population theorists (e.g., DeAngelis 1975; Hassell 1978; Abrams 1982, 1984). Recently, Arditi and coworkers have criticized the assumption of resource dependence on mainly empirical grounds (Arditi and Akçakaya 1990; Arditi and Berryman 1991; Arditi et al. 1991*a*, 1991*b*). As an alternative, Arditi and Ginzburg (1989) hypothesized that the functional response should depend on the ratio between resource and consumer densities.

In an attempt to find empirical support for their hypothesis, Arditi et al. (1991*a*) have compared a previously published pattern of *Daphnia* and phytoplankton abundances from a wide range of lakes (McCauley et al. 1988) with the predictions of resource-dependent and ratio-dependent differential equation consumer-resource models. Arditi et al. (1991*a*) concluded that a ratio-dependent model of the *Daphnia*-phytoplankton interaction was fully able to describe the observed relationship. They further suggested that the ratio-dependent model, because of its simplicity and mathematical convenience, should be preferable to alternative resource-dependent models, which needed to invoke mechanistic details of interactions with other components of the pelagic community in order to explain the observed abundance relationship between *Daphnia* and phytoplankton. In this comment, we argue that the ratio-dependent model proposed by Arditi et al. lacks any mechanistic foundation, that their way of testing the predictions of resource and ratio dependence is invalid, and that trophic interactions in lake communities are too complex to be explained by simple, two-dimensional consumer-resource models. Finally, we discuss, in a more general sense, the value of very simple, at best phenomenological, population models that are intended to satisfy pragmatic needs rather than to increase our insight into the mechanisms underlying the dynamics of natural populations.

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HAS RATIO DEPENDENCE A MECHANISTIC BASE?

Consumer-resource models of the Lotka-Volterra type deal with instantaneous rates of change, often combined with the assumptions of both homogeneous mixing of the interacting populations and an instantaneous connection between foraging and population dynamics (i.e., no time delays in the conversion of consumed resources into consumer offspring; Rosenzweig 1977). To circumvent these biologically problematic assumptions, Arditi et al. (1991*a*) suggested the ratio-dependent functional response as being an integrated expression of the per capita feeding rate over the whole, often spatially heterogeneous habitat and on the "slow" time scale of population dynamics. However, in the context of differential equations it appears mathematically incorrect to use the ratio of the *actual* densities of resources and consumers in order to introduce the effects of time delays into a system (Oksanen et al. 1992). Differential or difference equation models that directly include time delays predict consumer-resource dynamics and effects of enrichment radically different from those predicted by Arditi et al. (Oksanen et al. 1992).

It is true that spatial heterogeneity may create situations in which substantial proportions of the consumers and resources experience local population densities different from average ones and thus produce overall population dynamics that deviate from those of homogeneous systems (fig. 1; Hassell and May 1973; Free et al. 1977; but see Crowley 1981). However, spatial heterogeneity can be explicitly introduced into models of the Lotka-Volterra type as long as the effects of heterogeneity do not change with population densities (see, e.g., Tanner 1975; Holt 1984, 1987; McNair 1986). Furthermore, spatial heterogeneity imposes a cost of searching for resource patches to the consumers that, at low overall prey densities, might exceed the benefits gained from those patches (Murdoch and Oaten 1975). Thus, it is difficult to envision how spatial heterogeneity could create a situation in which a consumer population can maintain itself, or even grow, at very low densities of its resource. In the ratio-dependent models, however, the consumer isocline is predicted to go through the origin, which implies that consumers are able to show positive population growth at infinitely low resource densities (fig. 1). We conclude that, although ratio dependence in the functional response is intended to introduce the effects of temporal and spatial heterogeneities into consumer-resource interactions, there is no obvious mechanistic connection between ratio dependence and either time delays or spatial heterogeneity.

Arditi et al. (1991*a*) suggest that time delays and spatial heterogeneities, which, in turn, are assumed to cause ratio-dependent population dynamics, are intrinsic to the interaction between *Daphnia* and phytoplankton. In this case, it would seem logical to expect deviations from resource-dependent dynamics to occur in experimental tests of the isolated *Daphnia*-phytoplankton interaction. In their own experiments, Arditi et al. (1991*b*) have shown that the population dynamics of planktonic cladocerans like *Daphnia* and *Ceriodaphnia* conformed to the predictions of an entirely resource-dependent functional response. It then seems more than problematic that the authors "resolve" the contradiction between these results from an independent test of their assumption of ratio dependence

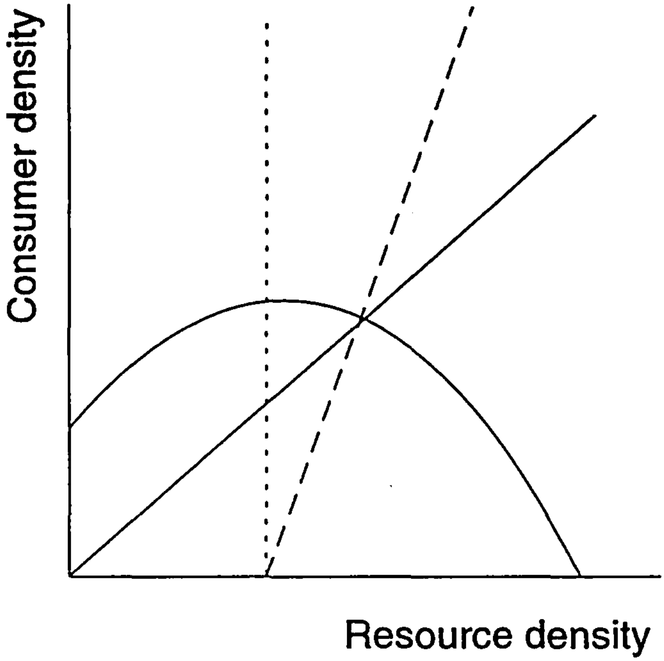

FIG. 1.—Phase plane of consumer and resource densities. The *straight lines* represent consumer isoclines from a ratio-dependent consumer-resource model (*solid, diagonal line*), a resource-dependent model (*dotted line*), and a model with "pseudointerference" (Free et al. 1977) in the consumer population (*dashed line*). For reference, an example of a resource isocline is also given (*solid, hump-shaped line*).

and the postulated existence of ratio-dependent dynamics in lakes, by claiming "that the growing conditions of *Daphnia* in the experimental containers were far more homogeneous than natural conditions in lakes" (Arditi et al. 1991*b*, p. 73).

DO BIOMASS CORRELATIONS ACROSS PRODUCTIVITY GRADIENTS SUPPORT RATIO-DEPENDENT MODELS?

Models based on resource-dependent and ratio-dependent functional responses make a number of different predictions about the response of consumer-resource systems to increased resource productivity. In the case of a strictly resource-dependent functional response, increasing resource productivity increases consumer density but not resource density, owing to the vertical position of the consumer isocline (Rosenzweig 1971; but see Oksanen et al. 1992; Abrams 1993). In the case of a ratio-dependent functional response, the consumer isocline is slanted, and increasing resource productivity leads to a proportional increase in both consumer and resource densities (Arditi and Ginzburg 1989). Furthermore, since ratio-dependent models predict that the consumer isocline goes through the origin, they also predict that the number of trophic levels in a community is independent of the system's primary productivity and that the biomasses of all

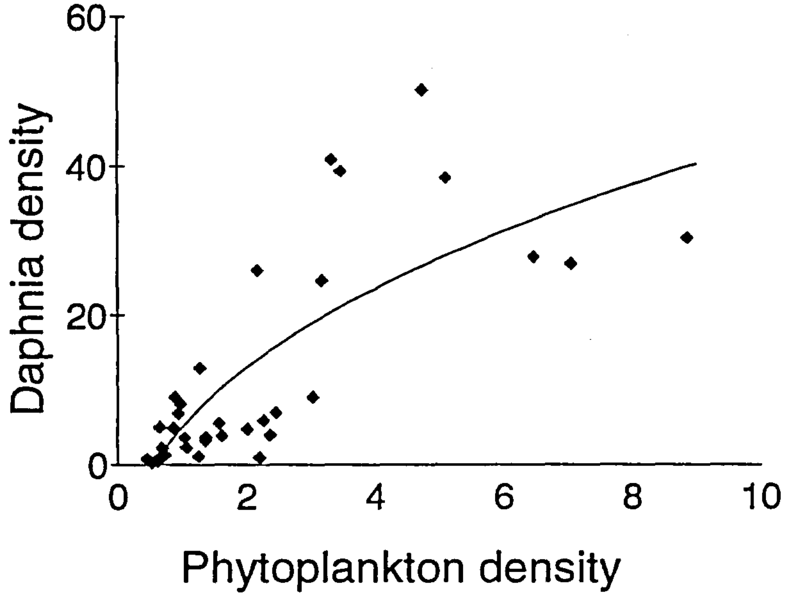

FIG. 2.—Relationship between the densities of phytoplankton (mg/L) and *Daphnia* (individuals/L) from the data set of 34 lakes published by McCauley et al. (1988). The *solid regression line* was obtained by fitting the model *Daphnia* = $\epsilon + \alpha(\text{phytoplankton})^{\beta}$ to the data.

trophic levels increase linearly with productivity. This view contrasts with the predictions from resource-dependent models, in which the number of trophic levels in a community is positively related to the system's primary productivity and in which the biomasses at each trophic level are related in a more stepwise manner to primary productivity (Smith 1969; Fretwell 1977; Oksanen et al. 1981).

Arditi et al. (1991*a*) tested the predictions of resource- and ratio-dependent models by regressing empirically derived densities of consumers on densities of their resources. The approach of Arditi et al. has, however, two serious problems. First, if data are to be used to test for model predictions, it is, of course, invalid to include the predictions to be tested into the assumptions of the test. Thus, while ratio-dependent models would predict a regression line that goes through the origin, this prediction cannot be tested using a regression model that *forces* the regression line through the origin (i.e., *Daphnia* = $\alpha[\text{phytoplankton}]^{\beta}$), as was done by Arditi et al. Using a less biased regression model (*Daphnia* = $\epsilon + \alpha\,[\text{phytoplankton}]^{\beta}$) gives a better fit with the data (adjusted $r^2 = 0.60$ vs. adjusted $r^2 = 0.56$ in the regression of Arditi et al.) and returns both a y intercept ($\epsilon = -23$, SE = 30) and a value of β ($\beta = 0.37$, SE = 0.30) that is different from the value of $\beta = 1$ predicted by ratio-dependent models (fig. 2).

Second, and more fundamentally, the regression approach has an obvious pitfall that has been disregarded by Arditi et al., as well as other authors (e.g., McQueen et al. 1986). Resource- and ratio-dependent models make sufficiently distinct predictions about biomass correlations only among communities with

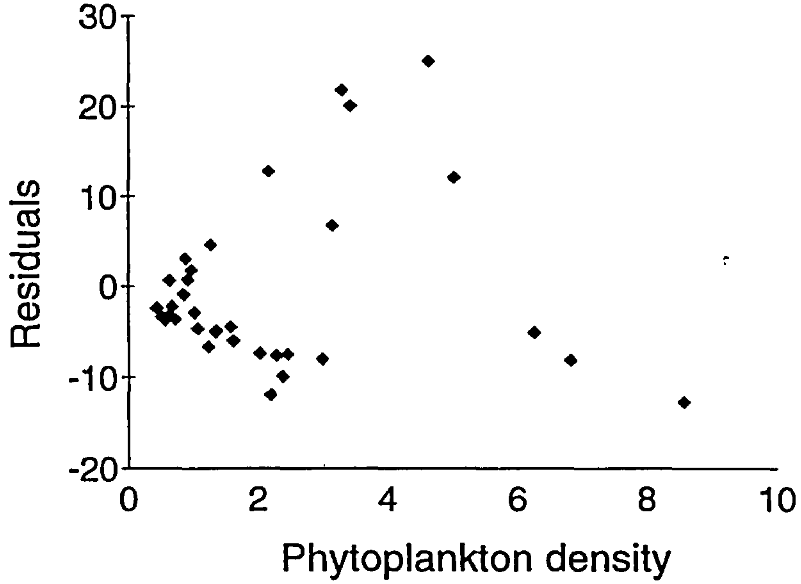

FIG. 3.–Residuals of the regression model *Daphnia* = $\alpha(\text{phytoplankton})^{\beta}$ applied by Arditi et al. (1991*a*) to the data set in fig. 2 (units of the axes as in fig. 2). Note that the distribution of residuals is not random. The relationship between phytoplankton density and residuals appears to be negative at phytoplankton densities less than 2.5 mg/L, positive at phytoplankton densities between 2.5 and 5 mg/L, and again negative at phytoplankton densities greater than 5 mg/L.

identical trophic structure. In contrast, if equilibrium biomasses are plotted against each other over large gradients of productivity, where resource-dependent models predict changes in the number of trophic levels (as was done by Arditi et al.), then both resource- and ratio-dependent models predict positive correlations between adjacent trophic levels (Mittelbach et al. 1988; Persson et al. 1988; Power 1992). Still, while ratio-dependent models predict simple linear correlations, resource-dependent models predict more stepwise relationships. In the noisy real world it might be hard to distinguish between the two predicted patterns with a regression approach (but see Oksanen et al. 1992). Nevertheless, an inspection of the residuals in the *Daphnia*-phytoplankton regression of Arditi et al. suggests that the data are more consistent with a stepwise relationship than a linear one (fig. 3). A more straightforward test of the model predictions would be to study the effects of enrichment while holding trophic structure constant. A surprisingly small number of studies have used this latter approach, all of which have given little support for the assumption of ratio dependence (Hansson 1992; Persson et al. 1992; Sarnelle 1992).

THE COMPLEXITY OF TROPHIC INTERACTIONS IN LAKES

Trophic interactions in the structurally simple pelagic zone of lakes have proven to be notoriously complex (Carpenter 1988), and it seems likely that the dynamics of system components, such as the *Daphnia*-phytoplankton interaction, cannot be understood in the context of simple two-species consumer-resource models. In line with this argument, recent attempts to include a variety of empirical observations into more mechanistic approaches to trophic interactions in lake communities have opened up some interesting new perspectives (McCauley et al. 1988; Mittelbach et al. 1988; Persson et al. 1988, 1992; Leibold 1989). All of these approaches have several features in common: (1) they explicitly account for the presence of size structure in aquatic populations, (2) they include more state variables than are present in two-species consumer-resource models, and, (3) even if resource dependence is assumed in the functional response, they predict positive correlations between phytoplankton and zooplankton biomasses in, at least, parts of the productivity gradient.

The presence of size structure in zooplankton, phytoplankton, and fish populations may profoundly affect consumer-resource interactions in aquatic communities. For example, explicit considerations of stage structure in population models of *Daphnia* and their algal food have indicated that system dynamics may, in parts of the parameter space, be driven by the physiological state of *Daphnia* individuals rather than by consumer-resource interactions (McCauley and Murdoch 1987; de Roos et al. 1992). Size structure in phytoplankton populations affects phytoplankton-zooplankton interactions primarily through its effects on size-specific foraging efficiencies of zooplankters. Leibold (1989) suggested that the biomass increase of large, "inedible" phytoplankton (algae >35 μm; Neill 1988; Leibold 1989), which is observed over large ranges of lake productivities (Watson and McCauley 1988), could account for positive correlations between *total* phytoplankton (edible + inedible fraction) and zooplankton biomasses (see also Abrams 1993). Positive correlations are also found between the abundance of *Daphnia* and the biomass of *edible* phytoplankton only (McCauley et al. 1988). McCauley et al. (1988) proposed that the inedible fraction of phytoplankton should interfere with the feeding mechanism of *Daphnia* and that the resulting negative relationship between the attack coefficient of *Daphnia* and productivity could, at least partly, account for such correlations. Mittelbach et al. (1988) advanced the idea that positive correlations between trophic levels in the pelagic zone of lakes could occur if resource limitation of littoral feeding size classes of fish prevented pelagic feeding size classes from efficiently tracking zooplankton prey populations. Similarly, Persson et al. (1988, 1992) suggested that positive correlations between trophic levels might result from competitive juvenile bottlenecks in the recruitment of pelagic piscivores. As a consequence of such bottlenecks, the proportion of piscivores in total pelagic fish biomass decreases from moderately to highly productive Scandinavian lakes (Persson et al. 1991), which suggests a decrease in predator regulation of planktivores with productivity in that part of the productivity gradient. This situation, in turn, might account for the observed increase in *Daphnia* death rates with productivity, which McCauley et al. (1988) suggested to be the single most important mechanism behind the covariance of *Daphnia* and phytoplankton biomasses. The view that *Daphnia* has the potential to control phytoplankton populations even at high nutrient levels and that positive correlations between *Daphnia* and phytoplankton are due to an increase in *Daphnia* death rates with productivity has been strongly supported by a recent survey of experimental manipulations of *Daphnia* from a wide range of algal productivities (Sarnelle 1992).

POSSIBILITIES AND LIMITATIONS OF PURELY PHENOMENOLOGICAL MODELS

Arditi and co-workers have advanced ratio-dependent consumer-resource models as an alternative to the resource-dependent models widely used in theoretical population biology. In their eyes, the virtues of ratio-dependent models are generality, mathematical simplicity, and the ability to predict observed biomass correlations between consumers and their resources. We have shown that for the case made by Arditi et al. (1991*a*)—that is, the *Daphnia*-phytoplankton interaction—the data do not fit the predictions from the ratio-dependent model. We have furthermore provided a number of mechanisms underlying trophic interactions in aquatic systems that all can produce positive correlations between consumers and resources while still assuming pure resource dependence in the functional responses of the individual consumer-resource interactions. The latter suggests that the debate over "resource-dependent" versus "ratio-dependent" models may not be a very productive controversy. There is little doubt that different forms of purely resource-dependent and of resource- *and* consumer-dependent models will be relevant to different situations, but the ratio-dependent models are only special cases of the latter type of models. In fact, the assumption that the resource and consumer dependence always enters as the ratio of the two is very specific, which greatly reduces the generality of the ratio-dependent model.

Arditi et al. (1991*a*) invoke common characteristics of many real consumer-resource interactions, such as time delays and spatial heterogeneities, in order to justify their assumption of ratio dependence in the functional response of the consumer. Nevertheless, Arditi et al. do not attempt to prove that time delays and spatial heterogeneities are, in fact, the causes of observed biomass correlations in real communities, nor is their assumption of ratio dependence in the functional response mechanistically related to time delays or spatial heterogeneities. Thus, the actual structure of the ratio-dependent model reflects a purely phenomenological approach to finding the best fit to data. However, the ambition to fit data as closely as possible (under the constraint that the predator isocline has to go through the origin) further weakens the generality of ratio-dependent models. Arditi et al. have to introduce an "interference constant," which may be highly organism or system specific, in order to account for data sets that do not fit the predictions of purely ratio-dependent models. Furthermore, the whole approach of Arditi et al. probably runs counter to the scientific intuition of many researchers who work for a deeper understanding of the processes that regulate ecological communities. If one is interested in the effects of time delays and spatial heterogeneity on consumer-resource interactions, it would seem most straightforward to investigate these effects through direct consideration of underlying mechanisms and patterns (see, e.g., Oksanen 1990; Oksanen et al. 1992). Such approaches need not always yield detailed, parameter-rich, and highly specific solutions.

Rather, a deeper understanding of the relative importance of different processes may enable us to find a level of ecological abstraction that optimally balances mechanistic detail against generality and predictive power (Tilman 1989).

In spite of their descriptive character and their limited generality, ratio-dependent models may still be useful tools for some purposes. For example, in special cases in which the outcome of complex population interactions is accurately described by a ratio-dependent two-species consumer-resource model, such a model may be preferable to more mechanistic approaches if the intention is to investigate higher-level processes. This is because mechanistic detail at the lower level might introduce an amount of complexity into the higher-level model that makes the latter mathematically intractable (Schoener 1986; Persson and Diehl 1990). It is, perhaps, not surprising that ratio-dependent expressions for the functional response have often been proposed "by workers pressed by the need of building models for practical purposes" (Arditi et al. 1991*a*, p. 1292). However, we recommend great caution in the use of ratio-dependent models for all purposes, including pragmatic ones. The use of simplified descriptions of lower-level phenomena in the analysis of higher-level processes can be appropriate only if the higher-level processes to be investigated do not strongly interact with the mechanisms that produce the lower-level phenomena. Even if this condition is fulfilled, it seems unlikely that a single term in simple two-species consumer-resource models should be able to describe adequately the "macroscopic" effects of such various factors as time delays, spatial heterogeneities, size structure, and populations other than the two considered. We thus seriously doubt whether ratio-dependent two-species consumer-resource models have sufficient predictive power to satisfy the needs of pragmatic modelers. They certainly do not fulfill the needs of researchers who attempt to *understand* the implications of time delays, spatial heterogeneity, or size structure for consumer-resource interactions.

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