

CONSEQUENCES OF RATIO-DEPENDENT PREDATION FOR STEADY-STATE PROPERTIES OF ECOSYSTEMS¹

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Abstract. Ratio-dependent and prey-dependent models of trophic interactions make very different predictions about the steady-state (equilibrial) properties of ecosystems, such as the response of equilibrium abundance and biomass of organisms in each trophic level to increased primary productivity or nutrient input. Prey-dependent theory predicts alternating positive, negative, and zero responses of trophic levels to increased productivity, whereas ratio-dependent theory predicts proportional increase in all trophic level biomasses. We analyzed data on the nutrient input and the biomasses of phytoplankton, zooplankton, and fish across lakes to distinguish between ratio-dependent and prey-dependent models. The results show parallel increases in all trophic levels as a result of increased nutrient input, demonstrating that natural systems are closer to ratio dependence than to prey dependence.

Key words: *bottom-up control; cascading effects; interference; lake trophic interactions; prey dependence; ratio dependence; top-down control; trophic biomass ratios.*

INTRODUCTION

In most fields of science, models and theories describing the dynamics of natural systems or processes are generalizations based on the prior *static* theories for these systems. The static (steady-state) properties have usually been described before the dynamic theories are developed. These properties establish the relationship among system components when they are in equilibrium. In physics, for example, Archimedes found the static properties of objects submerged in liquids long before theories of fluid mechanics were developed to describe how objects *move* in liquids. In ecology, on the other hand, dynamic theories (for example Lotka-Volterra models of population growth, predation, and competition) were developed without a solid static foundation. Large fluctuations in the abundances of organisms, which make the study of steady states extremely difficult on the time scale of human perception, probably distracted the attention of early theorists from equilibrial problems.

Experimental and field biologists, unlike theoreticians, did pay attention to equilibrial (steady-state) properties of ecosystems. These properties include relationships among abundances or biomasses of different trophic levels. Since ecological systems can rarely

be found in perfect equilibrium, these relationships are usually based on long-term averages. In this paper, we will summarize several studies and reanalyze several data sets, mostly from the last 10 yr, that establish empirical (and statistical) relationships among different trophic levels. Our aim is to show the discrepancies between the predictions of two different types of dynamic models (based on prey dependence and ratio dependence) and the observed patterns, and to demonstrate that the observed patterns can be better explained by ratio-dependent theory than by the traditional prey-dependent theory.

Prey dependence vs. ratio dependence

The general prey–predator model can be written as

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

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

where $f(N)$ is the *per-capita* rate of increase of the prey in the absence of predation and μ is the food-independent predator mortality, assumed to be constant. The trophic function $g(N,P)$ (also called the functional response) describes the amount of prey consumed per predator per unit time. In the predator equation (Eq. 1b), $eg(N,P)$ describes *per-capita* predator production

¹ For reprints of this Special Feature, see footnote 1, p. 1529.

(the numerical response), where e is the trophic efficiency. In traditional models it is always assumed that rate of consumption of prey by predator depends only on prey density (*prey-dependent* trophic function): $g = g(N)$. This formulation of the trophic function is based on the assumption that consumer density does not have any direct effects on the per-individual consumption rate, i.e., there is no interference among consumers. In fact, results of several studies point out that in most cases consumption rate decreases as the abundance of consumers increases, because they have to share the same resource among a larger number of consumers. A number of recent publications challenge the adequacy of the assumption of prey dependence (Arditi and Ginzburg 1989, Arditi and Akçakaya 1990, Arditi et al. 1991a, b, reviewed by Hanski 1991); and proposed that this sharing mechanism can be modeled by a *ratio-dependent* trophic function that is determined by the *per-capita* sources of the consumer: $g = g(N/P)$.

Arditi and Ginzburg (1989) argued that in order for a prey-predator model such as Eq. 1 to be internally consistent, the trophic function (the functional response) must be measured at the same time scale as that of population dynamics. At a behavioral time scale, the functional response of predators may in fact be independent of predator density. However, measuring the functional response at the slower time scale of population dynamics will in most cases introduce the sharing mechanisms described above, making the rate of predation (and the growth rate of the predator population) a function of the *per-capita* resources of the predator.

Prey- and ratio-dependent models show striking differences in the trophic abundances in food chains of increasing length in response to variations in primary productivity (Table 1). In the ratio-dependent model, all levels respond proportionately, while in the traditional prey-dependent model the responses differ depending on the trophic level and number of levels. The only level that responds proportionately to primary productivity is the last, top predator, level. The next to the last always remains constant, while the lower levels can even decrease with increasing primary production.

Particular models with ratio-dependent trophic functions have been studied by Ginzburg et al. (1971, 1974), Arditi (1975, 1979), Arditi et al. (1977, 1978), Getz (1984), Ginzburg (1986), and Akçakaya et al. (1988). Akçakaya (1992) developed a ratio-dependent predation model that can predict dynamic properties (such as cycle period) of hare-lynx cycles in Canada.

The “donor-controlled” models (see, e.g., Pimm 1982: 16) assume ratio dependence for the predator dynamics, while keeping the prey equation independent of predator density. This is a reasonable assumption

TABLE 1. Responses of food chains to primary input. Arrows show the variation of population equilibria to an increase of primary productivity, in food chains of length 2 to 5, in the two types of models. Symbols: \rightarrow no response; \propto proportionate response; \uparrow nonlinear increasing response; \downarrow nonlinear decreasing response (from Arditi and Ginzburg 1989).

Trophic level	Prey-dependence				Ratio-dependence			
	2	3	4	5	2	3	4	5
1	\rightarrow	\downarrow	\downarrow	\downarrow	\propto	\propto	\propto	\propto
2	\propto	\rightarrow	\downarrow	\downarrow	\propto	\propto	\propto	\propto
3		\propto	\rightarrow	\downarrow		\propto	\propto	\propto
4			\propto	\rightarrow			\propto	\propto
5				\propto				\propto

tion in cases where predators consume only dead or dying animals. For other types of predation, the relationship between the rate at which prey are killed and the rate at which predators reproduce is an essential property of the model (see Maynard Smith 1974: 24). This relationship defines the coupling or link between the functional and numerical responses (the “conservation” of the trophic energy flow). Evidence from a number of studies (see, for example, Slobodkin 1986 for hydras; Beddington et al. 1976 for numerous arthropods; and Coe et al. 1976 for large African herbivores) points out that this link can be modeled as a simple proportion between functional and numerical responses, as in Eq. 1. The proportion e is the conversion efficiency. The fact that predators do not consume all their prey is reflected in the numerical value of the efficiency parameter, which is always less than one. Normally, a minimum threshold reflecting maintenance needs should be subtracted from g in Eq. 1b, but this can be ignored since its effect can be incorporated into the predator death rate μ (Arditi and Ginzburg 1989).

Intermediate interference

The relationships among biomasses and productivities of various trophic levels can be explored by analyzing a three-level ecosystem model that is balanced (i.e., the rate of change of each trophic level set to zero) to examine the equilibrium (steady-state) properties of the system. Designating abundances of the three trophic levels as plants (P), herbivores (H), and carnivores (C), the following simple balance model will be utilized:

$$RP - DP - f\left(\frac{P}{H^\alpha}\right)H = 0 \tag{2a}$$

$$e_h f\left(\frac{P}{H^\alpha}\right)H - g\left(\frac{H}{C^\beta}\right)C = 0 \tag{2b}$$

$$e_c g\left(\frac{H}{C^\beta}\right)C - \mu C = 0 \tag{2c}$$

Here R is primary productivity, D is plant mortality rate, f is the rate of consumption of plants by an average herbivore, g is the rate of consumption of herbivores by an average carnivore, e_h and e_c are the efficiencies of herbivores and carnivores, respectively, in converting consumed material into reproduction, and μ is the mortality rate of carnivores.

The arguments of functions f and g proposed in the model (Eq. 2) generalize the traditional prey-dependent and the ratio-dependent cases by introducing parameters α and β , which measure the degree of interference among consumers while consuming resources. Traditional prey-dependent models correspond to $\alpha = \beta = 0$ and ratio-dependence results when $\alpha = \beta = 1$. In a paper specifically devoted to evaluating this interference parameter from experimental studies, Arditi and Akçakaya (1990) showed that in most cases the interference parameter is significantly different from zero; the estimates were often indistinguishable from one, but typically were less than one. This indicates a possible compromise between the two extreme views, closer to ratio dependence than to prey dependence. The proposed model (Eq. 2) with intermediate interference at both levels will produce responses that depend on the strength of interference.

Experimental and field evidence

The striking difference in the predictions of prey-dependent and ratio-dependent models for the static properties of ecosystems (Table 1) suggests a possible test: if the ratio-dependent theory is correct, ecosystems that have richer resources (but are otherwise similar) should exhibit higher equilibrium abundances on all trophic levels. On the other hand, if the prey-dependent theory is correct, they should exhibit alternating higher and lower abundances in different trophic levels.

The alternating pattern of abundances as predicted by the prey-dependent model also underlies the famous HSS hypothesis (Hairston, Smith, and Slobodkin 1960, Fretwell 1977, Oksanen et al. 1981). It may seem that there is evidence for this pattern in studies where "cascading" effects have been observed following an experimental manipulation of one of the trophic levels (see, for example, Power 1990). These cascading effects are alternating increases and decreases in the abundance or biomass of trophic levels depending on their position in the food chain relative to the manipulated trophic level. This observation has also been interpreted as "top-down" population control, a hypothesis stating that trophic biomasses are controlled from above by consumers, since any artificially induced increase in a trophic level results in a decrease of the biomass of the trophic level below it (initiating a cascading ef-

fect). In contrast, the "bottom-up" hypothesis states that trophic biomasses are controlled from below by producers.

A crucial point in the interpretation of these results with respect to various hypotheses and models is the importance of the experimental time scale. The predictions in Table 1 refer to static (steady-state; equilibrium) biomass and abundance, not to initial (dynamic) changes that follow an experimental manipulation. Actually, both prey-dependent and ratio-dependent models predict a "cascading" effect in the short term, i.e., before the biomasses of trophic levels settle into an equilibrium. Support for the top-down model usually comes from relatively short-term manipulations of predator populations in the same ecosystem (e.g., the same lake), whereas support for the bottom-up model comes from measurement from different ecosystems that are assumed to receive stable but different nutrient inputs (McQueen et al. 1986). The first type of experiment measures the short-term dynamic responses in a system that is perturbed away from the equilibrium, similar to the "pulse" perturbation defined by Bender, Case, and Gilpin (1984). Several authors have pointed out that top-down effects are usually observed in studies with short time scales and that these effects may not be sustained if the system is allowed to reach equilibrium (Carpenter et al. 1987, Carpenter 1988, Crowder et al. 1988, Mills and Forney 1988).

The type of manipulation that can distinguish between the predictions of prey-dependent and ratio-dependent models in Table 1 would change the level of nutrient input to a system and keep it at the new level until all trophic levels reach their new equilibria. This is similar to the "press" perturbation defined by Bender et al. (1984). It is difficult to carry out such an experiment because of the long time scale involved and because natural variation in trophic level biomasses may make the identification of the new equilibrium difficult. However, the second type of study mentioned above, which involves the measurement of biomasses from different ecosystems that are assumed to receive stable but different nutrient inputs, is in a sense a natural experiment of this type. In these studies the correlation among various trophic levels across ecosystems are measured. If these analyses include several years of data that are averaged for each ecosystem, the averages can be assumed to approximate the equilibrium (i.e., static) characteristics in a specific class of ecosystems (e.g., lakes). It is for this kind of regression that traditional prey-dependent models predict a mixture of positive, negative, and zero slopes depending on the trophic level and the chain length. Table 1 summarizes these predictions for the relationship between any trophic level and the nutrient input. Predictions about the relationship between any two trophic levels are similar:

prey-dependent models predict negative, zero, or positive slopes depending on the pair of trophic levels and on the food chain length, whereas ratio-dependent models predict proportional increases. The studies we summarize below and the analyses of trophic data in the next section demonstrate that the predictions of prey-dependent models are in total contradiction with empirical findings from terrestrial and aquatic ecosystem studies.

A worldwide comparison of forest ecosystems of increasing productivity shows a responding pattern both in plant and animal biomasses (Whittaker 1975: 224–226). Evidence supporting the ratio-dependent hypothesis is also provided by Ricklefs (1979: 623), who shows that wolf populations and their prey vary among localities in the same biomass ratio. The results of an experiment using an acarine predator-prey system in a complex environment (Bernstein 1981) also supports ratio dependence: when the numbers of prey and predators were varied with a constant ratio of 4:1, the number of prey eaten per predator did not vary significantly. These data are presented in Arditi and Ginzburg (1989) and Arditi, Ginzburg, and Akçakaya (1991).

McNaughton et al. (1989) compiled data on the primary productivity, secondary productivity and consumption, and herbivore biomass from studies of terrestrial ecosystems, including desert, tundra, temperate grassland, temperate successional old field, unmanaged tropical grassland, temperate forest, tropical forest, salt marsh, and agricultural tropical grassland. They incorporated data from 35–69 ecosystems for each variable. Their analysis showed that there is significant correlation between herbivore biomass and plant production.

In aquatic systems, comparison of trophic biomasses across lakes has shown that both zooplankton biomass and fish biomass are correlated with primary productivity (phytoplankton density) among lakes (McCauley and Kalff 1981, Jones and Hoyer 1982, Hanson and Peters 1984, Pace 1984). In addition, all three trophic levels are positively correlated with nutrient input as measured by phosphorus concentration (Deevey 1941, Yan and Strus 1980, Hanson and Leggett 1982, Jones and Hoyer 1982, Prepas and Trew 1983, Hanson and Peters 1984, Pace 1984, Stockner and Shortreed 1985, Persson et al. 1988; see next section for detailed analyses). Arditi et al. (1991a) also found a positive correlation between abundance of *Daphnia* and its algal food supply across lakes.

Clearly, all these findings are in complete contradiction with the predictions of the prey-dependent models. They support ratio dependence in a qualitative way, since correlations among the long-term averages of the biomasses of trophic levels across ecosystems are always positive. In the next section, we present

more data on the statistical relationships among different trophic levels in lake ecosystems.

METHODS AND RESULTS

Most ecosystem-level studies that concentrate on trophic interactions have been on lakes, probably because lakes provide well-defined and more or less closed systems. Some of these studies have recently been reviewed by Hanson and Peters (1984), Kerfoot and DeAngelis (1989), McQueen, Post, and Mills (1986), McCauley, Murdoch, and Watson (1988), McCauley and Kalff (1981), Stockner and Shortreed (1985), and Carpenter (1988). We used these references as a starting point to collate the physical and biological properties of 175 lakes. Since different studies used slightly different methods, most of the data were analyzed separately, except for the nutrient-phytoplankton relationship (see below). For each of these studies, a logarithmic regression was performed:

$$\log_{10}L2 = a + b \log_{10}L1,$$

where $L1$ and $L2$ are two trophic levels (including nutrients). The parameter b (the slope of log-log regression) is an estimate of the *reciprocal* of the interference coefficient, α or β , if $L1$ and $L2$ are the top two consecutive trophic levels. Some of the statistical results reported by original authors included repeated measurements from the same lake, so all the data sets were reanalyzed by first taking the average values for each lake and including each lake as a single data point. The original papers that were used in some studies could not be found. As a result we did not re-analyze these data and the results (marked by asterisk in Table 2) are as reported by the authors. The lakes in these studies are not included in the pooled sample for the nutrient-phytoplankton relationship (Fig. 1).

The regression analyses summarized in Table 2 show that all but one of the slopes are significantly greater than zero, two-thirds of the slopes (10 out of the 15 for which the standard error is either calculated or was available) are not significantly different from one, and one-third are significantly less than one. These results demonstrate that all trophic levels respond in the same direction to an increase in productivity, and the response is in most cases proportional.

DISCUSSION

One of the important differences of ratio-dependent theory from traditional prey-dependent theory is its prediction of increases in the biomasses of *all* trophic levels as a result of an increase in productivity. The evidence from both terrestrial and aquatic ecosystems reviewed in the *Introduction* and data on the trophic structure of lake ecosystems analyzed in *Methods and results* show that this expectation is correct. Moreover,

TABLE 2. Results of regression analyses for each pair of trophic levels. b is the slope of log-log regression, n is the sample size, and r^2 is the proportion of variance explained by the regression. The units are: Nutrient: total phosphorus (mg/m^3); Phytoplankton: chlorophyll a density (mg/m^3); Zooplankton: biomass (mg/m^3); crustacean biomass in Yan and Strus (1980); Fish: biomass (kg/ha).

Trophic levels	b ($\bar{X} \pm 1 \text{ SE}$)	n	r^2	Reference	Fig.
Nutrient vs. Phytoplankton	1.335 ± 0.205	25	0.648	Jones and Hoyer (1982)	1
	1.249 ± 0.133	49	0.669	Hanson and Peters (1984)	
	1.091 ± 0.093	12	0.932	Pace (1984)	
	1.061 ± 0.145	26	0.691	Prepas and Trew (1983)	
	1.013 ± 0.204	19	0.590	Stockner and Shortreed (1985)	
	0.997 ± 0.280	32	0.297	Deevey (1941)	
	0.884 ± 0.045	119	0.770	Data base in this study	
Nutrient vs. Zooplankton	1.632 ± 1.371	11	0.136	Yan and Strus (1980)	2
	0.917 ± 0.083	49	0.723	Hanson and Peters (1984)	
	0.643 ± 0.084	12	0.855	Pace (1984)	
Phytoplankton vs. Zooplankton	0.719 ± 0.112	17	0.856	McCauley and Kalff (1981)*	3
	0.534 ± 0.067	49	0.572	Hanson and Peters (1984)	
	0.554 ± 0.084	12	0.812	Pace (1984)	
Nutrient vs. Fish	1.566 ± 0.431	25	0.365	Jones and Hoyer (1982)	4
	0.708	18	0.75	Hanson and Legett (1982)*	
Phytoplankton vs. Fish	1.210 ± 0.137	25	0.77	Jones and Hoyer (1982)	5

* These results are given as they were reported by the authors.

the slopes of log-log relationships among trophic levels estimated for these systems demonstrate that the natural systems are closer to ratio dependence than to prey dependence. Specifically, none of the systems shows the kind of alternating positive, negative, and zero slopes predicted by the traditional prey-dependent models.

It has been proposed (see Gatto 1991) that proportionality of equilibria can also be attained by assuming that the predator mortality increases as a quadratic function of predator abundance (e.g., μC^2 instead of μC in Eq. 2c). This would represent a type of density-dependent mortality to the consumer population that

is independent of resource limitations or interactions with the food supply. Besides restricting the type of density dependence to non-resource-related mechanisms, this argument also appears weak on theoretical grounds. First, it produces the proportionality of equilibria only if all functional responses (e.g., f and g in Eq. 2) are linear relationships (i.e., Holling's type I functional response: $f(P) = aP$, $g(H) = bH$). When non-linear functional responses (arising from handling time, or a limit to the maximum rate of consumption) are introduced, the equilibria are no longer proportional. Second, the mortalities should be precisely quadratic;

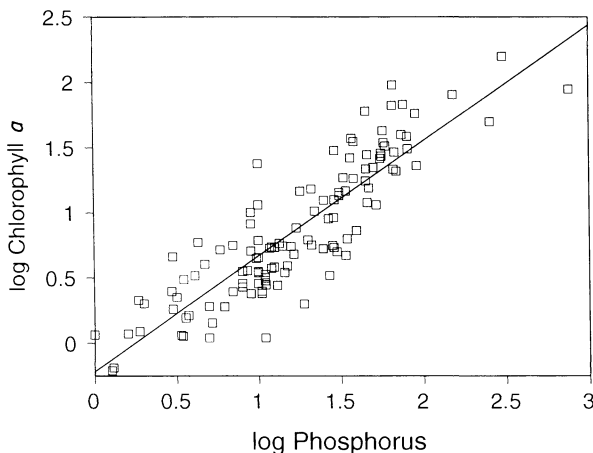


FIG. 1. Relationship between nutrient concentration (total phosphorus in mg/m^3) and phytoplankton density (chlorophyll a density in mg/m^3) in the lakes in the data base compiled from studies listed in Table 2.

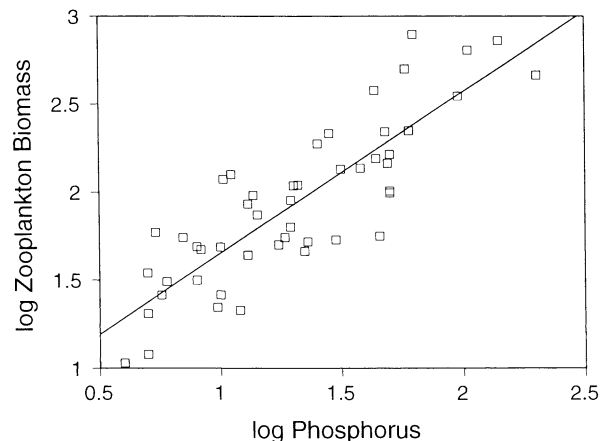


FIG. 2. Relationship between nutrient concentration (total phosphorus in mg/m^3) and zooplankton biomass (mg/m^3) for lakes in Hanson and Peters (1984).

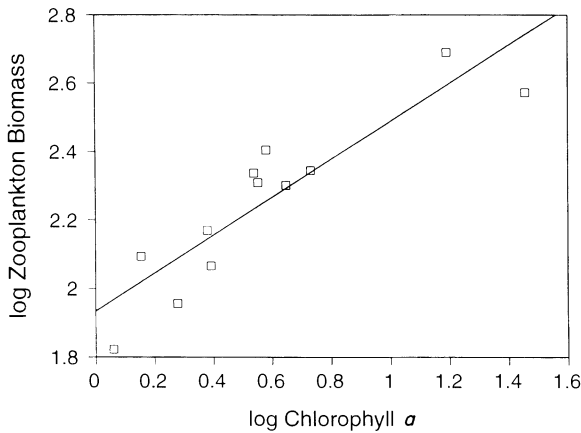


FIG. 3. Relationship between phytoplankton density (chlorophyll *a* density in mg/m³) and zooplankton biomass (mg/m³) in the data set of Pace (1984).

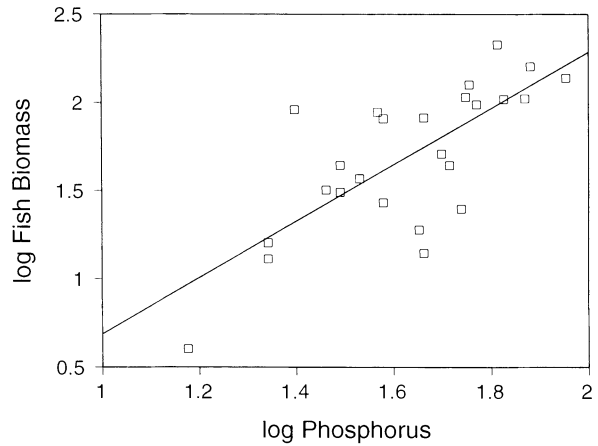


FIG. 4. Relationship between nutrient concentration (total phosphorus in mg/m³) and fish biomass (kg/ha) in the data set of Jones and Hoyer (1982).

if they are combinations of linear and quadratic terms, the proportionality, again, does not follow.

The biological mechanism that gives rise to ratio dependence can be summarized as interference. Arditi and Ginzburg (1989) and Arditi and Akçakaya (1990) give more detailed discussions of biological mechanisms leading to ratio-dependent functional responses. As noted above the relationships among trophic equilibria are not always exactly proportional, indicating that the interference constants introduced in Eq. 2 are not exactly equal to 1 (ratio dependence), although the definitely differ from 0 (prey dependence). This suggests that the more complicated model (Eq. 2) intermediate between prey and ratio dependence, may offer a more realistic framework for modeling trophic interactions. Another functional form (see, e.g., DeAngelis et al. 1975) that can incorporate intermediate levels of interference is

$$f(P, H) = \frac{P}{a + bP + cH}$$

where *a*, *b*, and *c* are constants. This function approximates the ratio-dependent functions of Eq. 2 when consumer (herbivore, *H*, in this example) density is high and approximates prey-dependent, type II functional response when consumer density is low. Since the biological mechanism for ratio dependence is interference, it is expected to be less dominant in systems where consumer densities are low. In addition, we would also expect that the equilibria may not be exactly proportional when consumer densities are very high and other limiting factors besides food come into play. (This case cannot be represented by the above equation.) It is therefore particularly interesting to see that, within the range of the densities in natural lake ecosystems,

the predictions of ratio-dependent theory hold quite well, especially compared to those of the prey-dependent models.

Another explanation for the intermediate values of slopes in the previous section is the effect of physical properties of lakes. Pridmore et al. (1985) analyzed the relationship between chlorophyll *a* and phosphorus in New Zealand lakes. As in most such studies (see previous section and Table 2) they found a slope of greater than one (1.50) for the log-log relationship, indicating an interference coefficient of less than one. However, when they included mean depth of lakes in the regression, the partial slope of chlorophyll *a*-phosphorus relationship was decreased to 1.00, indicating perfect ratio dependence. Similar effects of mean depth on chlorophyll *a* were seen in other studies (Ramberg 1979 and Ahl 1980; reviewed by Smith 1990).

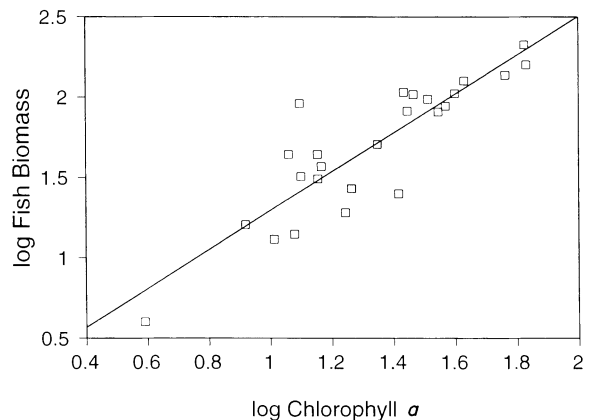


FIG. 5. Relationship between phytoplankton density (chlorophyll *a* density in mg/m³) and fish biomass (kg/ha) in the data set of Jones and Hoyer (1982).

If the proposed model (Eq. 2) is a realistic description of trophic interactions, a more detailed analysis of data using this model may give additional information about the exact form of the equations. Specifically, fitting the model (Eq. 2) to data on steady-state properties of ecosystems to estimate α and β will provide partial information about the structure of the functions f and g . In addition, analyses of short-term (dynamic, "pulse"-type) experimental data with this model will furnish further details on these trophic functions.

In conclusion, statistical analysis of the steady-state biomasses of trophic levels across lakes produces results that are consistent with ratio-dependent theory, which predicts positively correlated, proportional increases of all trophic levels as the primary productivity or the nutrient input increases. In contrast, traditional prey-dependent theory predicts a mixture of uncorrelated and positively or negatively correlated responses, depending on the length of the food chain. In addition to resolving the contradiction between observed patterns and predictions of traditional models, the proposed model also reconciles the dichotomy of top-down vs. bottom-up control. Both views have validity, since according to the proposed model, all levels may contribute to the observed pattern, depending on the interference coefficients in the trophic functions f and g .

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