12

The Relative Importance of Resource Limitation and Predator Limitation in Food Chains

Craig W. Osenberg and Gary G. Mittelbach

Introduction

Over 30 years ago, Hairston et al. (1960) published a short, insightful, and controversial paper (see also Slobodkin et al. (1967)) that attempted to explain how resource limitation and predator limitation varied among different trophic levels. Hairston et al. restricted their arguments to terrestrial systems with three trophic levels; however, Fretwell (1977) later extended Hairston et ál.'s verbal model to systems with greater (or lesser) numbers of trophic levels. The basic argument presented by Hairston et al. and Fretwell was that one process (i.e., resource limitation or predator limitation) should dominate at a given trophic level and that the identity of this process should alternate among adjacent trophic levels: e.g., if a consumer trophic level was resource-limited, then the trophic levels comprising its resources and predators should both be predator-limited.

The simple ideas put forward by Hairston et al. have given rise to a remarkable number of empirical and theoretical studies, and thus represent an important foundation for much of ecology (Fretwell, 1987; Schoener, 1989; Kingsolver and Paine, 1991). There is wide latitude, however, in interpreting the predictions of Hairston et al. and applying them to specific ecological systems. This has caused difficulties both for testing the theory and refining it. One of our goals in this paper is to clarify what is meant when a trophic level (or population) is said to be limited by a given process, and to suggest how limitation may be operationally defined and measured in nat-

ural systems. We use data from our studies of aquatic communities to estimate the relative magnitudes of resource and predator limitations at three trophic levels within a single system. Last, we review data from whole lake surveys to evaluate how the relative importance of resource limitation and predator limitation might vary over productivity gradients. We begin with a brief discussion of previous evaluations of Hairston et al.'s model. We do not address the more general problems concerned with the definition of trophic levels (Polis, 1991) and the debate about the organisms and systems to which Hairston et al. originally defined their problem (e.g., Hairston (1985)).

Previous Tests of Hairston et al.'s Model

Connell (1983), Schoener (1983), and Sih et al. (1985) attempted to test Hairston et al.'s (1960) predictions by compiling the proportion of published studies that showed *statistically significant* effects of competition (Connell, 1983; Schoener, 1983) or predation (Sih et al., 1985) on a target species (not trophic levels as a whole). These studies assumed that the predictions of Hairston et al. equated to competition (or predation: Sih et al. (1985)) occurring significantly more (or less) often among carnivores and primary producers than among herbivores in three-trophic-level systems. Statistical significance, however, does not measure the biological importance, or strength, of a process, nor does it exclude the importance of other processes

(Jones and Matloff, 1986; Yoccoz, 1991). Indeed, it is likely that many processes simultaneously limit populations (Quinn and Dunham, 1983; Mittelbach et al., 1988), and the relative importance of a factor can only be ascertained by comparing the effect of a particular process (which is a quantitative measure of magnitude, not statistical significance) relative to the effect of other processes. Gurevitch et al. (1992) make this point in a more recent review (although their analysis confounds the magnitude of the effect with the variability observed among replicate plots). Combining results from different systems can also obscure the importance of particular processes operating *within* systems due to inherent differences among the systems studied: e.g., due to variation in the number of trophic levels or productivity (Oksanen et al., 1981; Fretwell, 1977, 1987; Oksanen, 1988; Schoener, 1989).

Trophic cascades (e.g., Power (1990), Spiller and Schoener (1990), and Vanni et al. (1990)) have also been viewed as evidence supporting Hairston et al.'s model and the general importance of top-down processes (Schoener, 1989; Power, 1990). While trophic cascades clearly reveal that predators influence prey dynamics, the occurrence of trophic cascades says little about the relative importance of limitation imposed by predators vs. resources. This would require documentation of the response of each trophic level to changes in the density of predators as well as changes in the density of resources. Trophic cascades provide only weak support for Hairston et al.'s ideas because trophic cascades are predicted by many models that dynamically link adjacent trophic levels (e.g., Oksanen et al. (1981), Arditi and Ginzburg (1989), and Kretzschmar et al. (1993)) but make very different assumptions (see discussion in Ginzburg and Akcakaya (1992)).

Part of the difficulty in assessing the validity of Hairston et al.'s hypothesis is that their model was verbal and open to a variety of interpretations. Thus, an important step in the development of ideas that originated with Hairston et al. came in 1981, when Oksanen et al. (1981) developed a multitrophic level model that extended the three-level system examined by Rosenzweig (1973). Oksanen et al. (1981) were motivated by the earlier work of Hairston et al. (1960) and Fretwell (1977), and their study is often referred to as a formalization of Hairston et al.'s model (e.g., Schmitz (1992)). However, the model developed by Oksanen et al. (1981) incorporates processes in ways that often differ from the verbal model set forth by Hairston et al. Most importantly, Oksanen et al.'s (1981) model includes the simultaneous effects of resources and predators on the growth of any consumer population (or trophic level); thus, each trophic level is simultaneously limited by predators and resources. While Hairston et al. clearly recognized that a given trophic level could be simultaneously limited by both resources and predators (see Slobodkin et al. (1967)), they argued that a single process would strongly dominate at any particular trophic level and that the identity of this process would alternate across trophic levels. It is this prediction that is most often viewed as the salient feature of Hairston et al.'s model and it is this prediction that we examine below.

Limitation, Regulation, and Control

The terms *limitation, regulation,* and *control* are often used interchangeably in describing the interactions between trophic levels and in discussing the predictions of Hairston et al. (e.g., Ehrlich and Birch (1967), Slobodkin et al. (1967), and Persson et al. (1988)). However, we suggest these terms actually refer to different aspects of the processes that influence population abundance and dynamics and that it would be wise to distinguish between them. For example, regulation occurs when there is a locally stable equilibrium, and results from the operation of density-dependent processes. Perturbations to a system can be dampened through time due to the action of these regulatory processes (Figure 12.1). In contrast, we suggest that control is often used to refer to factors that set the equilibrium at a particular density (or more generally affect density); these factors need not operate in a density-dependent fashion. Perturbations to a system can shift the system to a new equilibrium if a controlling factor was affected by the perturbation (Figure 12.1). Thus, regulation and control refer to processes that cause a population or trophic level to be at a particular density and therefore necessarily involve the action of direct and
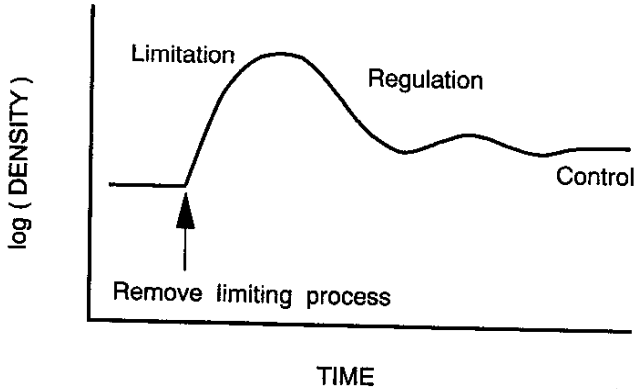
TIME

Figure 12.1. Graphical illustration of *limitation, regulation,* and *control.* Preceding a perturbation, the idealized system is at equilibrium and the density (measured as numbers or biomass per unit area) of the focal population (or trophic level) is constant. At the point of the perturbation (indicated by the arrow and representing, for example, the removal of predators or the addition of resources), the growth of the focal population increases. This increased growth rate results in an increase in density, but the growth rate eventually decreases due to feedbacks within the system (e.g., due to reductions in other resources or increases in other sources of mortality). The feedbacks arise from the existence of an equilibrium and represent regulation. Eventually, the system reequilibrates due to the balancing of gains and losses that control, or determine, the specific density at which equilibration occurs (which will probably not be the same equilibrium density that occurred prior to the perturbation). The initial increase can be used to estimate limitation (Equation (3)), and in this example (with natural rates of change equal to zero due to the equilibrium) is equal to the slope of the curve (i.e., $d[\log(density)]/d(time)$) immediately following the perturbation.

indirect effects mediated throughout the community over a variety of time scales (Schaffer, 1981; Bender et al., 1984).

Limitation, on the other hand, is a simpler concept and can be defined without reference to the potential complexities inherent in regulation (Figure 12.1). Limitation is the extent to which a population's, or trophic level's, per capita growth rate is depressed by the action of a particular factor (e.g., resource availability or predation risk). Operationally, limitation can be measured by quantifying the increase in a population's per capita growth rate following the removal of a particular form of limitation (e.g., after the addition of surplus resources, or the removal of predators). Limitation necessarily focuses on the change in growth rate (e.g., as assessed by a change in abundance) over short timescales so that the influence of a specific process can be isolated from other processes (whose influences will eventually change as other components of the system change). Ideally, this requires measurement of an instantaneous response to a perturbation, or

a sustained manipulation in which the single source of limitation is removed while all other factors that could influence population growth are held constant (Figure 12.2).

In this chapter, we focus our attention on processes that limit the dynamics and abundance of populations or trophic levels (we are not explicitly interested in effects on community structure: cf. Menge and Sutherland (1976)). Although these restrictions do not necessarily agree will all discussions of Hairston et al., they are consistent with the overall theme of the original papers (Hairston et al., 1960; Slobodkin et al., 1967).

The Estimation of Limitation Under Field Conditions

To quantify limitation, we desire an index that isolates the effect of a limiting factor (e.g., predation, or suboptimal resource availability) on per capita population growth. We begin with an exponential model of population growth to describe dynamics of a focal
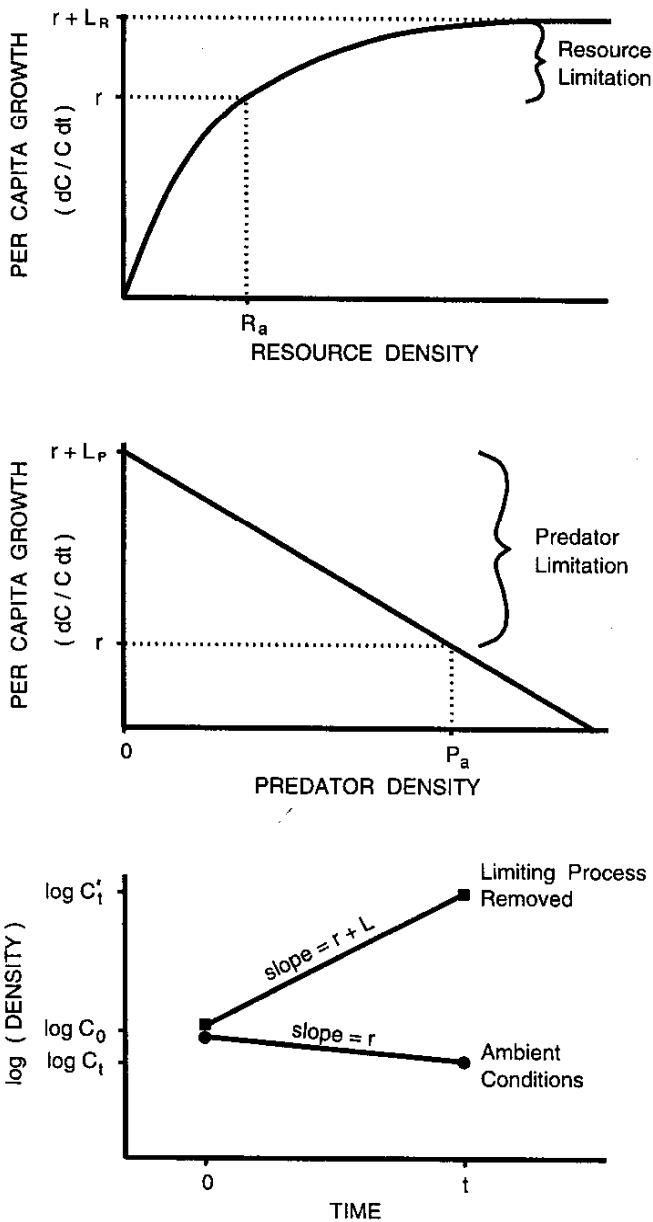
Figure 12.2. Graphical representations of resource limitation (top panel), predator limitation (middle panel), and limitation as assessed through a field experiment (bottom panel). Top: The per capita growth of a consumer trophic level (or population) under different resource densities (assuming all other species remain at their ambient densities). As resource density (R) increases, per capita growth of the consumer (dC/Cdt) increases, but eventually asymptotes to the maximum rate that the consumer is capable of given its physiological limitations and the influences of all other species within the system. The per capita growth of the consumer is equal to r under ambient conditions (i.e., when $R = R_a$), and $r + L_R$ in the absence of resource limitation. Although we represent the x-axis as resource density, it is best considered a combined index of resource abundance and quality. Middle: The per capita growth of the consumer under different predator densities (P). As predator density increases from zero, the per capita growth rate of the consumer declines from its maximum, $r + L_p$, to r (at the ambient density of the predator, P_a), to even lower values at greater predator densities. Bottom: Limitation can be estimated in the field as the difference between the per capita growth under natural conditions, r, and conditions in which limitation from the focal process has been eliminated, $r + L$. Thus, limitation can be estimated via Equation (3), which yields the difference in slope between the trajectories in the two treatments.

population (or trophic level), which we call the consumer, and assume that its density (C) changes over a short interval of time according to

$$C_t = C_0 e^{rt}, \qquad (1)$$

in sites with ambient densities of resource, predators, and other species, and according to

$$C_t' = C_0 e^{(r+L)t} \qquad (2)$$

in sites where the limiting process does not act (i.e., has been removed). C_0 is the density of the consumer population (or trophic level) at the start of the experiment (and is assumed equal in the two treatments); C_t is the density under ambient conditions after t days; C_t' is the density in the absence of the limiting process after t days; r is the population's instantaneous (i.e., per capita) growth rate under ambient conditions; and $r+L$ is the per capita growth rate in the absence of the limiting factor. Therefore, L is a quantitative estimate of limitation, representing the decrement in population growth due to limitation imposed by the process being studied. If the initial density (C_0) and duration (t) are the same for the two treatments, L can be estimated as:

$$L = [\ln(C_t') - \ln(C_t)]/t \qquad (3)$$

This expression can be adjusted if the initial density or duration vary among the sites. The index of limitation is superficially similar to others that have been proposed (e.g., to quantify interaction strength (Paine, 1992)), but differs in that it is explicitly defined using a model of the effect of the limiting process on per capita population growth (see Wilson and Tilman (1993) for an analogous index involving plant competition).

Operationally, addition of surplus (and high-quality) resources leads to estimation of resource limitation (L_R: Figure 12.2a,c), whereas removal of predators leads to the estimation of predator limitation (L_P: Figure 12.2b,c). In future studies, it would also be possible to assess the importance of the interaction between two (or more) processes by simultaneously eliminating both sources of limitation and comparing the response with that predicted from the additive responses following elimination of each process separately. Here, we restrict our analyses to the effects of single factors.

Under ideal situations, growth rates should be measured soon after elimination of the limiting process, and in the absence of changes in the abundances of other species (i.e., without confounding effects of feedbacks through other components of the system). This is rarely possible, however, due to time lags in the responses of populations, inherent difficulties in performing such idealized manipulations, and problems in measuring very small short-term responses. Caution must therefore be exercised in any application of this approach and precautions taken to help ensure that direct effects are isolated from longer-term feedbacks.

To deal with some of these problems, we use biomass instead of abundance to calculate density. This enabled us to aggregate across organisms within a trophic level that might have very different body sizes (making total abundance a problematic measure of density), and also to equate the responses of a trophic level to changes in predators and resources (which over short timescales can act through different vital rates). The use of biomass to better equate effects on mortality, fecundity, and individual growth is, in part, justified because fecundity is often proportional to body mass (Peters, 1983), so that short-term changes in biomass provide a good surrogate of eventual changes in population density.

Estimates of Limitation in an Aquatic Food Chain

We use the preceding definitions of limitation (Equation (3), Figure 12.2c) to estimate the strength of resource limitation and predator limitation for three trophic levels in a single natural system, Lawrence Lake, a well-studied oligotrophic lake in southwest Michigan. Although most of the data we use were collected for other purposes (and are therefore not ideally suited to measure limitation), we can think of no consistent biases inherent in these studies that should influence the qualitative outcome of our analyses. We view this analysis as a first cut at quantifying the rela-

tive magnitudes of resource and predator limitation within a system, and it is our hope that it will stimulate future and better studies designed specifically to estimate limitation at multiple trophic levels.

Most of the data were extracted from studies of littoral zone interactions in Lawrence Lake. The food chain in this habitat includes epiphytic algae (consisting primarily of closely adhering microalgae attached to rooted aquatic plants: Burkholder (1986)), invertebrate grazers (dominated by gastropods: Mittelbach (1981)), microcarnivorous fishes (dominated by the bluegill, *Lepomis macrochirus,* and pumpkinseed sunfish, *L. gibbosus:* Werner et al. (1977)), and piscivorous fishes (consisting almost entirely of largemouth bass, *Micropterus salmoides:* Werner et al. (1977)). Here we focus on the first three of these trophic levels.

Resource limitation of algae was quantified by comparing the accumulation of algal biomass in control sites with sites in which phosphorus, nitrogen, and potassium fertilizer was added in excess (Osenberg, 1988, 1989). Responses were restricted to approximately one month following fertilization in order to minimize the feedback between fertilization and snail grazing; snail biomass increased following the fertilization, which eventually decreased algal growth. Predator limitation of algae was quantified using gradients of gastropod densities imposed directly via manipulation of gastropods or indirectly via manipulation of molluscivorous fish (Osenberg, 1988, 1989).

Resource limitation in gastropods was assessed by quantifying the change in gastropod biomass in fertilized plots, which had very high algal biomass (Osenberg, 1988, 1989). Gastropod biomass was measured at the end of one month to isolate the direct response to increased resources from indirect effects that arose following a shift toward grazer-resistant algae (Osenberg, 1988). Predator limitation of invertebrates was estimated from experiments that manipulated fish density. The effect of fish on snails was estimated in a nearby lake (Palmatier Lake), which has a similar density of the dominant molluscivore (pumpkinseed sunfish) as Lawrence Lake (Osenberg et al., 1988). Other experiments suggest pumpkinseeds account for all demonstrable effects of predators on snail mortality rates (Osenberg, unpublished data). Effects of fish on other invertebrates was estimated from a field experiment in Lawrence Lake in which the biomass of invertebrates was quantified over a gradient of sunfish densities (Mittelbach, 1988). Comparison of invertebrate biomass at natural fish densities with those estimated in the absence of fish was used to quantify predator limitation (using Equation (3)).

Resource limitation of fish was estimated using data from Mittelbach (1986) and Werner and Hall (1988) in which they introduced small bluegills and pumpkinseeds into ponds previously lacking fish and thus with high densities of invertebrate prey. We quantified resource limitation by comparing these individual growth rates with growth rates of similar-sized fish living in Lawrence Lake (Osenberg and Mittelbach, unpublished data). Growth rates of other species of fishes strongly covary with growth rates of littoral feeding bluegill and pumpkinseed (Osenberg et al., 1994), so these estimates are likely to apply to the entire fish community (which is dominated by bluegill: > 60% of total fish biomass). Predator limitation of these fishes was assessed in several studies in which bluegill (or pumpkinseed) biomass or numbers were monitored in experimental ponds that either lacked largemouth bass or had a density and size structure of bass similar to Lawrence Lake (Werner et al., 1983; Werner and Hall, 1988; Turner and Mittelbach, 1990).

In each experiment predator and resource densities were altered in particular ways. It is possible that different alterations of resources (i.e., food) might have produced even stronger responses. It is also possible that removal of additional predator taxa might have increased the responses in the predation experiments. Without extensive data on the nutritional requirements of consumers and the relative impact of different predators, ideal experiments testing for resource and predator limitation cannot be achieved. Therefore the estimates of limitation for trophic levels in Lawrence Lake might be somewhat biased; however, in all cases, resource limitation was assessed by creating what appeared to be close to ideal food conditions for the consumers, and in each predation experiment, the most obvious and putatively important predator was manipulated.

Table 12.1 Resource limitation and predator limitation for three trophic levels in Lawrence Lake. Limitation was estimated from previous studies and unpublished data using Equation (3) or a slight modification. Limitation is given in units of per day and is the amount by which the biomass specific growth rate increased when resources were greatly increased or predator density was reduced to zero. For each trophic level, we report the mean, range (in parentheses), and number of studies that permitted estimation of limitation. Analysis of variance (using log-transformed data) revealed significant main effects of trophic level (fish vs. invertebrates vs. algae: $F_{2,10}=9.4$, $P=.005$) and limitation source (resource vs. predator: $F_{2,10}=20.4$, $P=.001$), but no statistically significant interaction ($F_{2,10}=2.15$, $P=.17$). Qualitative results were unaffected by data transformation.

Trophic level	Resource limitation	Predator limitation
Fish	0.025 (0.012–0.038) 4	0.0011 (0.0001–0.0031) 4
Invertebrates	0.042 (0.032–0.052) 2	0.0056 (0.0035–0.0077) 2
Algae	0.098 (0.088–0.107) 2	0.0309 (0.0098–0.0519) 2

Four general conclusions emerge from these analyses (Table 12.1).

1. As indicated in many of the original studies, resources and predators simultaneously limited each of these trophic levels; estimates of limitation exceeded zero.
2. However, these factors did not operate to similar degrees. Each trophic level showed a greater change in biomass in response to resource addition than in response to the removal of predators. Therefore, resource limitation was more severe than predator limitation for each trophic level. Data for the fourth trophic level, largemouth bass, suggest that it is also strongly resource-limited throughout its life history (Gilliam, 1982; Osenberg et al., 1994; Olson et al., 1995). No doubt our studies underestimated the combined effect of all predators (e.g., the predators we focused on make up between approximately 50% and 90% of predator biomass for the three trophic levels: Mittelbach (1981) and Werner et al. (1977)), but even incorporating a correction of a twofold increase in predator limitation would not reverse the patterns we observed (which, of course, also include possible under-

estimates of resource limitation). Thus, each trophic level appears to be more severely resource-limited than predator-limited; this pattern is not consistent with the predictions of Hairston et al.

3. There was a tendency for the relative importance of resource limitation to be greater at the higher trophic levels (Table 12.1). Addition of resources led to a 25-fold greater increase in biomass production for sunfish than did the removal of predators. Similar comparisons for invertebrates and epiphytes showed eightfold and threefold variation, respectively. We believe the most likely explanation is that we more severely underestimated resource limitation for the lowest trophic level (i.e., algae) due to numerical (or growth) responses of grazers following nutrient enrichment.

4. The magnitude of limitation (e.g., response to resource addition or removal of predators) was strongest at the lowest trophic levels. This pattern is probably a simple consequence of the expression of limitation in terms of biomass-specific production rates; smaller organisms have greater production to biomass ratios (Peters, 1983) and lower tro-

phic levels (consisting of smaller organisms) might therefore yield higher absolute estimates of limitation.

The Effect of System Productivity

Many of the recent studies motivated by Hairston et al. (1960) are concerned with patterns of abundance across productivity gradients (e.g., Persson et al. (1992), Mittelbach and Osenberg (1993), and Wootton and Power (1993)). Limitation (as discussed above) has been largely ignored in these treatments, although it plays a central role in many of the interpretations about the importance of top-down and bottom-up processes. For example, it is well known that the biomass of adjacent trophic levels tends to increase along productivity gradients in lakes (as assessed by the concentration of phosphorus, the limiting nutrient in most lakes) (see summaries in McQueen et al. (1986) and Ginzburg and Akcakaya (1992)). Because the biomass of resources and predators both increase with system productivity (but see Persson et al. (1988)), it is possible that resource limitation decreases and predator limitation increases along these productivity gradients. It might therefore be argued that our results for Lawrence Lake, which is a relatively unproductive (oligotrophic) lake, might not be generally applicable and that the importance of resource limitation would be ameliorated in more productive systems.

In the absence of studies of limitation conducted in lakes of different productivity, we used an indirect approach to assess if the relative importance of resource and predator limitation change along a natural productivity gradient. Observations from lake surveys suggest that trophic-level biomass increases as a power function of system productivity. Therefore, we assumed that the biomass of the focal trophic level (C, for consumer) and the biomass of the next higher trophic level (P, for predator) increase with system productivity (G) according to:

$$C \propto G^a, \qquad (4)$$

$$P \propto G^b, \qquad (5)$$

where a and b are fitted constants describing the rate at which consumer and predator biomass increase with system productivity.

Next, we assumed (as in standard Lotka-Volterra models) that the per capita (where per capita $\equiv$ per unit biomass) death rate of the focal (consumer) trophic level is proportional to predator density. Then, at equilibrium, the per capita birth rate (B: i.e., per capita production or turnover rate) of the consumer must balance this mortality rate. To get the total production (or turnover, T) of consumers, we multiply consumer biomass, C, by the consumer's per capita turnover rate, B:

$$T = CB \propto G^a G^b = G^{a+b}. \qquad (6)$$

That is, if the consumers and predators are in equilibrium, we expect the total production of consumers (T) to increase in proportion to the product of the rate of increase of consumer biomass (Equation (4): G^a) and the rate of increase of predator biomass (Equation (5): G^b, which is assumed to be proportional to the mortality imposed by the predator trophic level, which equals B).

We surveyed the literature to obtain estimates of the scaling relationships for the biomass and production of trophic levels along system productivity gradients. Total phosphorus (TP) concentration was the metric typically reported in these papers, although phosphorus loading may be a more appropriate index of system productivity. Because total phosphorus concentration and phosphorus loading are likely proportional to one another (Vollenweider et al. 1980), results obtained using TP should be similar to those that would be obtained using loading. Data were obtained for three trophic levels: algae (epiphytic and planktonic algae), invertebrates (zooplankton and benthos), and fishes. Although most data came from limnetic habitats, the data from littoral habitats showed very similar patterns (e.g., compare Cattaneo (1987) and Watson et al. (1992)).

Based upon this literature survey, we estimated the rate at which consumer production should increase with lake productivity (using Equation (6)), by summing the average scaling exponents for the biomass of the focal and next higher trophic levels. We then compared these estimates with the scaling exponent ob-

Table 12.2.   Scaling of trophic level biomass and production to system production. Scaling exponents are the slopes of least squares regression of log (biomass or production) versus log (total phosphorus concentration, TP). In several cases, least squares regressions were available for parameters other than TP (e.g., for primary production against algal biomass); these estimates were corrected by multiplying by the coefficient observed between the intermediate parameter (e.g., algal biomass) and TP. For each relationship, we indicate the mean exponent, standard deviation (in parentheses), and the number of relationships found in the literature survey. Results for fish production are not indicated (—) because data for piscivore biomass and fish production were not readily available. Regression results, or data, were taken from Beaver and Crisman (1991), Brylinsky (1980), Brylinsky and Mann (1973), Cattaneo (1987), del Giorgio and Peters (1993), Downing et al. (1990), Hanson and Leggett (1982), Hoyer and Jones (1983), Jones and Bachmann (1976), Jones and Hoyer (1982), Morgan (1980), Ostrofsky and Rigler (1987), Pace (1986), Quiros (1990a, 1990b), Rasmussen (1988), Watson and McCauley (1988), Watson et al. (1992), Yurk and Ney (1989), and studies cited in Table 2 of McQueen et al. (1986).

	Scaling Exponent		
	Biomass	Production	
Trophic level	Observed	Predicted	Observed
Fish	0.74	—	—
	(0.55)		
	7		
Invertebrates	0.74	1.48	1.00
	(0.14)		(0.22)
	10		4
Algae	1.14	1.88	1.19
	(0.22)		(0.26)
	17		6

served between total production of the focal trophic level and system productivity (i.e., TP).

For algae and invertebrates, production increased more slowly than predicted by Equation (6) (Table 12.2). Indeed, production increased at rates similar to that observed for the biomass of the focal trophic level, suggesting that a unit of biomass does not turn over at appreciably higher rates in more productive systems. Increased "predator" biomass does not seem to translate into higher mortality rates of consumers, nor does increased "resource" biomass translate into higher birth rates of consumers. Therefore, this crude analysis suggests that the relative strengths of predator and resource limitations do not change appreciably along this gradient of system productivity.

Limitation, Trophic-Level Heterogeneity, and Timescale

Our analyses, although preliminary, indicate consistent and strong resource limitation acting on adjacent trophic levels within a single system and among systems that vary in overall productivity. Our experimental results suggest that although predation (including herbivory) has documentable negative effects on consumer biomass, the impact of resource limitation is greater than the impact of predator limitation at all trophic levels. These patterns are not predicted by the model of Hairston et al. (1960), nor are they implied in more contemporary studies of "top-down control" (Oksanen et al., 1981; Oksanen, 1988; Schoener, 1989; Power, 1990). However, as noted by early critics of Hairston et al. (Murdoch, 1966; Ehrlich and Birch, 1967), trophic levels consist of species that vary in their vulnerability and utility to predators: e.g., many plants species (or plant parts) are inedible to herbivores (Sinclair, 1975; White, 1978; Rhoades, 1985; Sinclair et al., 1985; Hunter and Price, 1992). If higher trophic levels also are dominated by predator-resistant taxa, then this feature might explain the prevalence of resource limitation (vs. predator limitation) at all trophic levels.

Indeed, in freshwater systems predators are known to restrict the types of prey that coexist with them (Thorp, 1986). For exam-

ple, the most dramatic effects of fish (including local extinction of prey) are seen when fish are experimentally (or accidentally) introduced into previously fishless situations (e.g. Brooks and Dodson (1965), Crowder and Cooper (1982), and McPeek, 1990). Therefore, the prey that coexist with fish are relatively invulnerable to fish predation, and although predators can have great effects on some prey species, the most abundant taxa are often the least sensitive to predation (Vanni, 1987a; Mittelbach, 1988; Osenberg, 1988). Herbivores also may facilitate the development of grazer-resistant algal communities (Cattaneo and Kalff, 1986; Vanni, 1987b; but see Sarnelle (1993)). In addition, experiments and observational studies demonstrate that piscivores cause shifts toward relatively invulnerable prey species: e.g., prey fishes with spines and deep bodies (Tonn and Magnuson, 1982; He and Wright, 1992; see also Bronmark and Miner (1992)).

Thus, the activity of predators tends to create prey communities in which the co-occurring prey are less affected by predation. These relatively invulnerable prey often compensate for the higher mortality of vulnerable prey and may build up dense populations even in the presence of predators. If prey overlap in resource use, then resource limitation should be transmitted to all prey species, including those most susceptible to predation. Because these shifts in community composition can occur at each of the trophic levels, the relative importance of predation and resource limitation does not necessarily "flip-flop" as predicted by Hairston et al. Instead, the development of predation-resistant taxa at each trophic level can maintain resource limitation throughout the ecosystem.

The presence of invulnerable prey might also help explain the persistence of resource limitation in productive systems that contain high biomass of "predators" (and "resources"). For example, it has been commonly observed that algal communities in more productive systems are typically dominated by relatively inedible species (e.g., see Cattaneo (1987) for epiphyton and Trimbee and Prepas (1987) and Watson et al. (1992) for phytoplankton). Thus, the higher biomass of grazers in these systems does not necessarily translate into higher per capita mortality rates for the entire algal trophic level. Indeed,

Watson et al. (1992) suggested that increasing biomass of grazers only directly affects the smallest (i.e., edible) algae, which makes up a smaller proportion of total algal biomass in more productive lakes. Although the best available data come from studies of algae, studies of zooplankton also suggest shifts toward less vulnerable species in more productive systems (Bays and Crisman, 1983; Mills and Schiavone, 1982; but see Pace (1986)). Thus, while a small component of a trophic level might incur increased losses to predators as productivity increases, the bulk of the trophic level is invulnerable and, as a result, has a greater biomass but a similar per capita turnover rate in systems with high (vs. low) productivity.

If species composition changes across productivity gradients, as most available data suggest, then several caveats are in order with regard to the study of trophic-level responses to increased productivity. First, our conceptual understanding of food web dynamics needs to progress beyond models based on abstractions that represent trophic levels by a single species (e.g., Rosenzweig (1973) and Oksanen et al. (1981)). Most natural trophic levels consist of many species that vary in many important aspects of their ecology, and therefore differ in their responses to predators, resources, and other environmental factors. Recent work has demonstrated how heterogeneity within a single trophic level, derived from population stage structure (Osenberg et al. 1992, Briggs, et al. 1993, Mittelbach and Osenberg 1993) or the presence of edible and inedible species (Leibold, 1989; Abrams, 1993; Kretzschmar et al., 1993), can lead to patterns of abundance and dynamics not predicted by simpler models. Future efforts should attempt to incorporate heterogeneity at more than one trophic level (Power, 1992; Strong, 1992).

Second, timescale of response becomes critically important as we seek explanations for patterns produced among sites that vary in environmental conditions (e.g., system productivity). Experiments conducted over short timescales are useful in revealing processes operating within systems (e.g., quantifying the magnitude of limitation), but potentially are misleading if used to try to recreate patterns observed over larger scales. For example, experimentally manipulating produc-

tivity within a system may lead to one pattern of response in the short term, but a very different pattern of response over the long run (as species composition within the community changes in response to changing levels of resources and predators) (Power et al., this volume). Thus, we need to exercise care when using short-term experiments to try and recreate systemwide patterns (e.g., Leibold (1989) and Wootton and Power (1993)). Experimental manipulations of productivity, unless conducted over very long periods (on the order of decades in many cases), may isolate the wrong processes by missing not only the numerical responses of higher trophic levels (with long generation times) but also shifts in species composition, which may require generations to play out.

Finally, there needs to be a more explicit link between theory and empirical tests. In particular, models (both verbal and mathematical) need to be explored more rigorously for predictions that can be tested in field situations. Also, field experiments are needed in which responses to predator removals and responses to resource addition are simultaneously and systematically assessed for different species and trophic levels within the same ecosystem. This approach will only yield significant insights if the models and empirical tests are stated within a clear framework that defines critical assumptions, including those related to timescale and trophic-level composition. The seminal work of Hairston et al. (1960) may continue to provide a cornerstone in the foundation of ecology, but only if we move beyond it by developing more explicit and mechanistic models that predict patterns based on the processes that create and maintain them.

Acknowledgments

References

Abrams, P. A. 1993. Effect of increased productivity on the abundances of trophic levels. *American Naturalist* 141:351–371.

Arditi, R. and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: Ratio-dependence. *Journal of Theoretical Biology* 139:311–326.

Bays, J. S. and T. L. Crisman. 1983. Zooplankton and trophic state relationships in Florida lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1813–1819.

Beaver, J. R. and T. L. Crisman. 1991. Importance of latitude and organic color on phytoplankton primary productivity in Florida lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1145–1150.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: Theory and practice. *Ecology* 65:1–13.

Briggs, C. J., Nisbet, R. M., and W. W. Murdoch. 1993. Coexistence of competing parasitoid species on a host with a variable life cycle. *Theoretical Population Biology* 44:341–373.

Bronmark, C. and J. G. Miner. 1992. Predator-induced phenotypical change in body morphology in crucian carp. *Science* 258:1348–1350.

Brooks, J. T. and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28–35.

Brylinsky, M. 1980. Estimating the productivity of lakes and reservoirs. In *The Functioning of Freshwater Ecosystems*, eds. E. D. Le Cren and R. H. Lowe-McConnell, pp. 411–453. Cambridge University Press, Cambridge, U.K.

Brylinsky, M. and K. H. Mann. 1973. An analysis of factors governing productivity in lakes and reservoirs. *Limnology and Oceanography* 18:1–14.

Burkholder, J. M. 1986. Seasonal dynamics, alkaline phosphatase activity and phosphate uptake of adnate and loosely attached epiphytes in an oligotrophic lake. Ph.D. Dissertation. Michigan State University, East Lansing, MI.

Cattaneo, A. 1987. Periphyton in lakes of different trophy. *Canadian Journal of Fisheries and Aquatic Sciences* 44:296–303.

Cattaneo, A. and J. Kalff. 1986. THe effect of

grazer size manipulation on periphyton communities. *Oecologia* 69:612–617.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *American Naturalist* 122:661–696.

Crowder, L. B. and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813.

Del Giorgio, P. A. and R. H. Peters. 1993. Balance between phytoplankton production and plankton respiration in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 50:282–289.

Downing, J. A., C. Plante, and S. Lalonde. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1929–1936.

Ehrlich, P. R. and L. C. Birch. 1967. The balance of nature and population control. *American Naturalist* 101:97–107.

Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine* 20:169–185.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? *Oikos* 50:291–301.

Gilliam, J. G. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Ph.D. Dissertation. Michigan State University, East Lansing, MI.

Ginzburg, L. R. and H. R. Akcakaya. 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. *Ecology* 73:1536–1543.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140:539–572.

Hairston, N. G. 1985. The interpretation of experiments on interspecific competition. *American Naturalist* 125:321–325.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421–425.

Hanson, J. M. and W. C. Leggett. 1982. Empirical prediction of fish biomass and yield. *Canadian Journal of Fisheries and Aquatic Sciences* 39:257–263.

He, X. and R. A. Wright. 1992. An experimental study of piscivore-planktivore interactions: Population and community responses to predation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1176–1183.

Hoyer, M. V. and J. R. Jones. 1983. Factors affecting the relation between phosphorus and chlorophyll *a* in midwestern reservoirs. *Canadian Journal of Fisheries and Aquatic Sciences* 40:192–199.

Hunter, M. D. and P. W. Price. 1992. Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.

Jones, J. R. and R. W. Bachmann. 1976. Prediction of phosphorus and chlorophyll levels in lakes. *Journal of the Water Pollution Control Federation* 48:2176–2182.

Jones, J. R. and M. V. Hoyer. 1982. Sportfish harvest predicted by summer chlorophyll-*a* concentration in midwestern lakes and reservoirs. *Transactions of the American Fisheries Society* 111:176–179.

Jones, D. and N. Matloff. 1986. Statistical hypothesis testing in biology: A contradiction in terms. *Journal of Economic Entomology* 79:1156–1160.

Kingsolver, J. G. and R. T. Paine. 1991. Theses, antitheses, and syntheses. In *Foundations of Ecology*, eds. L. A. Real and J. H. Brown, pp. 309–317. University of Chicago Press, Chicago.

Kretzschmar, M., R. M. Nisbet, and E. McCauley. 1993. A predator-prey model for zooplankton grazing on competing algal populations. *Theoretical Population Biology* 44:32–66.

Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134:922–949.

McPeek, M. A. 1990. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. *Ecology* 71:83–98.

McQueen, D. J., J. R. Post, and E. L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1571–1581.

Menge, B. A. and J. P. Sutherland. 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* 110:351–369.

Mills, E. L. and A. Schiavone, Jr. 1982. Evaluation of fish communities through assessment of zooplankton populations and measures of lake productivity. *North American Journal of Fisheries Management* 2:14–27.

Mittelbach, G. G. 1981. Patterns of invertebrate size and abundance in aquatic habitats. *Canadian Journal of Fisheries and Aquatic Sciences* 38:896–904.

Mittelbach, G. G. 1986. Predator-mediated habitat use: Some consequences for species interactions. *Environmental Biology of Fishes* 16:159–169.

Mittelbach, G. G. 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology* 69:614–623.

Mittelbach, G. G. and C. W. Osenberg. 1993. Stage-structured interactions in bluegill: Consequences of adult resource variation. *Ecology* 74:2381–2394.

Mittelbach, G. G., C. W. Osenberg, and M. A. Leibold. 1988. Trophic relations and ontogenetic niche shifts in aquatic ecosystems. In *Size-Structured Populations: Ecology and Evolution*, eds. B. Ebenman and L. Persson, pp. 219–235. Springer-Verlag, Berlin.

Morgan, N. C. 1980. Secondary production. In *The Functioning of Freshwater Ecosystems*, ed. E. D. Le Cren and R. H. Lowe-McConnell, pp. 247–340. Cambridge University Press, Cambridge, U.K.

Murdoch, W. W. 1966. Community structure, population control, and competition—A critique. *American Naturalist* 100:219–226.

Oksanen, L. 1988. Ecosystem organization: Mutualism and cybernetics or plain Darwinian struggle for existence? *American Naturalist* 131:424–444.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240–261.

Olson, M. H., G. G. Mittelbach, and C. W. Osenberg. 1995. Competition between predator and prey: Resource-based mechanisms and implications for stage-structured dynamics. *Ecology* (in press).

Osenberg, C. W. 1988. Body size and the interaction of fish predation and food limitation in a freshwater snail community. Ph.D. Dissertation. Department of Zoology, Michigan State University, East Lansing, MI.

Osenberg, C. W. 1989. Resource limitation, competition and the influence of life history in a freshwater snail community. *Oecologia* 79:512–519.

Osenberg, C. W., G. G. Mittelbach, and P. C. Wainwright. 1992. Two-stage life histories in fish: The interaction between juvenile competition and adult performance. *Ecology* 73:255–267.

Osenberg, C. W., M. H. Olson, and G. G. Mittelbach. 1994. Stage-structure in fishes: Resource productivity and competition gradients. In *Theory and Application in Fish Feeding Ecology*, eds. D. J. Stouder, K. L. Fresh, and R. J. Feller. pp. 151–170. University of South Carolina Press, Columbia, South Carolina.

Osenberg, C. W., E. E. Werner, G. G. Mittelbach, and D. J. Hall. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: Environmental variation and the importance of ontogenetic niche shifts. *Canadian Journal of Fisheries and Aquatic Sciences* 45:17–26.

Ostrofsky, M. L. and F. H. Rigler. 1987. Chlorophyll-phosphorus relationships for subarctic lakes in western Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 44:775–781.

Pace, M. L. 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. *Limnology and Oceanography* 31:45–55.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355:73–75.

Persson, L., G. Andersson, S. F. Hamrin, and L. Johansson. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. In *Complex Interactions in Lake Communities*, ed. S. R. Carpenter, pp. 45–65. Springer Verlag, Berlin.

Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1992. Trophic interactions in temperate lake ecosystems: A test of food chain theory. *American Naturalist* 140:59–84.

Peters, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, U.K.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist* 138:123–155.

Power, M. E. 1990. Effects of fish in river food webs. *Science* 250:811–814.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology* 73:733–746.

Quinn, J. F. and A. E. Dunham. 1983. On hypothesis testing in ecology and evolution. *American Naturalist* 122:602–617.

Quiros, R. 1990a. Predictors of relative fish biomass in lakes and reservoirs Argentina. *Canadian Journal of Fisheries and Aquatic Sciences* 47:928–939.

Quiros, R. 1990b. Factors related to variance of residuals in chlorophyll-total phosphorus re-

gressions in lakes and reservoirs of Argentina. *Hydrobiologia* 200/201:343–355.

Rasmussen, J. B. 1988. Littoral zoobenthic biomass in lakes, and its relationship to physical, chemical, and trophic factors. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1436–1447.

Rhoades, D. F. 1985. Offensive-defensive interactions between herbivores and plants: Their relevance in herbivore population dynamics and ecological theory. *American Naturalist* 125:205–238.

Rosenzweig, M. L. 1973. Exploitation in three trophic levels. *American Naturalist* 107:275–294.

Sarnelle, O. 1993. Herbivore effects on phytoplankton succession a eutrophic lake. *Ecological Monographs* 63:129–149.

Schaffer, W. 1981. Ecological abstraction: The consequences of reduced dimensionality in ecological models. *Ecological Monographs* 51:383–401.

Schmitz, O. J. 1992. Exploitation in model food chains with mechanistic consumer-resource dynamics. *Theoretical Population Biology* 41:161–183.

Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240–285.

Schoener, T. W. 1989. Food webs from the small to the large. *Ecology* 70:1559–1589.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: A review of field experiments. *Annual Review of Ecology and Systematics* 16:269–311.

Sinclair, A. R. E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. *Journal of Animal Ecology* 44:497–520.

Sinclair, A. R. E., H. Dublin, and M. Borner. 1985. Population regulation of Serengeti Wildebeest: A test of the food hypothesis. *Oecologia* 65:266–268.

Slobodkin, L. B., F. E. Smith, and N. G. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. *American Naturalist* 101:109–124.

Spiller, D. A. and T. W. Schoener. 1990. A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. *Nature* 347:469–472.

Strong, D. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747–754.

Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. *Oikos* 47:75–82.

Tonn, W. M. and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* 63:1149–1166.

Trimbee, A. M. and E. E. Prepas. 1987. Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae with emphasis on Alberta lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1337–1342.

Turner, A. M. and G. G. Mittelbach. 1990. Predator avoidance and community structure: Interactions among piscivores, planktivores, and plankton. *Ecology* 71:2241–2254.

Vanni, M. J. 1987a. Effects of food availability and fish predation on a zooplankton community. *Ecological Monographs* 57:61–88.

Vanni, M. J. 1987b. Effects of nutrients and zooplankton size on the structure of a phytoplankton community. *Ecology* 68:624–635.

Vanni, M. J., C. Luecke, J. F. Kitchell, Y. Allen, J. Temte, and J. J. Magnuson. 1990. Effects on lower trophic levels of massive fish mortality. *Nature* 344:333–335.

Vollenweider, R. A., W. Rast, and J. Kerekes. 1980. The phosphorus loading concept and great lakes eutrophication. In *Phosphorus Management Strategies for Lakes*, eds. R. C. Lochr, C. S. Martin, and W. Rast, pp. 207–234. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

Watson, S. and E. McCauley. 1988. Contrasting patterns of net- and nanoplankton production and biomass among lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 45:915–920.

Watson, S., E. McCauley, and J. A. Downing. 1992. Sigmoid relationships between phosphorus, algal biomass, and algal community structure. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2605–2610.

Werner, E. E., J. G. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 684:1540–1548.

Werner, E. E. and D. J. Hall. 1988. Ontogenetic habitat shifts in the bluegill sunfish (*Lepomis macrochirus*): The foraging rate-predation risk tradeoff. *Ecology* 64:1525–1539.

Werner, E. E., D. J. Hall, D. R. Laughlin, D. F. Wagner, L. A. Wilsmann, and F. C. Funk. 1977. Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Research Board of Canada* 34:360–370.

White, T. C. R. 1978. The importance of a relative

shortage of food in animal ecology. *Oecologia* 33:71–86.

Wilson, S. D. and D. Tilman. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74:599–611.

Wootton, J. T. and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain., *Proceedings of the National Academy of Sciences* 90:1384–1387.

Yoccoz, N. G. 1991. Use, overuse and misuse of significance tests in evolution and ecology. *Bulletin of the Ecological Society of America* 72:106–111.

Yurk, J. J. and J. J. Ney. 1989. Phosphorus-fish community biomass relationships in southern Appalachian reservoirs: Can lakes be too clean for fish? *Lake Reservoir Management* 5:83–90.