

# SPECIES TURNOVER AND THE REGULATION OF TROPHIC STRUCTURE

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## ABSTRACT

Trophic structure, the partitioning of biomass among trophic levels, is a major characteristic of ecosystems. Most studies of the forces that shape trophic structure emphasize either “bottom-up” or “top-down” regulation of populations and communities. Recent work has shown that these two forces are not mutually exclusive alternatives, but efforts to model their interaction still often yield unrealistic predictions. We focus on the problems involved with modeling situations in which community composition, including both the number of trophic levels and the species composition within a trophic level, can change. We review the development of these ideas, emphasizing in particular how compositional change can alter theoretical expectations about the regulation of trophic structure. A comparison of studies on the effects of predators and resource productivity in limnetic ecosystems reveals an intriguing disparity between the results of manipulative experiments and those of correlational studies. We suggest that this contrast is a result of the difference in the temporal scales operating in the two types of studies. Ecosystem-level variables may appear to approach an equilibrium in short-term press experiments; however, processes such as invasion and extinction of species will not have time to play out in most such experiments. We found that the responses of ecosystems to short-term experimental treatments involve less change in species composition than is found in natural communities that have diverged in response to local conditions over longer periods. We argue that the results of short-term experiments support the predictions of models in which

the species pool does not change, whereas correlational studies among systems support theories that incorporate compositional change.

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### *Introduction*

The interplay of forces that shape community structure has fascinated ecologists at least since Darwin (31). Elton (41), in particular, developed the notion that feeding relations in combination with energetic constraints and the diversification of organisms into functional roles could elucidate many aspects of community structure, including the partitioning of organisms into trophic levels (i.e. Elton's "pyramid of numbers"). Since then, many have attempted to explain how feeding relations among species influence major aspects of community structure. Trophic structure, defined here as the partitioning of biomass into trophic levels and "guilds," is perhaps the most obvious aspect of community structure related to the transfer of energy (in the form of fixed carbon and materials) implied by feeding relations (41, 83, 104).

Currently two artificially distinct perspectives attempt to explain variation in the trophic structure of ecosystems. The first, influenced by the perspectives of Elton (41) and Lindeman (83), assumes that major features of ecosystems are regulated primarily from the "bottom up" (99, 174, 175). This view suggests that the biomass of organisms at any trophic level is a function of the productivity of their resource base. Two predictions emerge from this approach (99): that more productive ecosystems will have more trophic levels, and that the biomass of organisms at all trophic levels will increase with the basal productivity of the ecosystem. Though these arguments have intuitive appeal, they are at odds with the predictions of the simplest mathematical formulations of predator-prey interactions that include any dynamic feedback from consumers to their resources.

Alternatively, a "top-down" approach focuses on how the number of trophic levels in a system influences partitioning of biomass among all the trophic levels. This view was most forcefully argued by Hairston, Smith, & Slobodkin (54), hereafter referred to as HSS (and further elaborated by Fretwell—44). Top-down forces have received renewed attention in aquatic systems, especially due to the work of Carpenter, Kitchell, and their collaborators (23, 25), and because of the potential for biomanipulation (purposeful management of fish populations) to alleviate the symptoms of lake eutrophication (65, 147). Based on a dualistic assumption that a given trophic level is regulated either by resource competition or by predation, HSS argued that the number of trophic levels functioning in an ecosystem determines its trophic structure. Plants are expected to dominate in ecosystems with odd numbers of trophic levels, whereas herbivores will dominate in ecosystems with an even number of levels. Based

in part on previous work in lake eutrophication (142), Carpenter & Kitchell (23) acknowledged a large role for nutrient loading in lake ecosystems. They used the same fundamental approach as HSS to argue that the abundance of secondary carnivores accounts for much of the variation in plant and herbivore biomass in lakes that is not explained by nutrient levels.

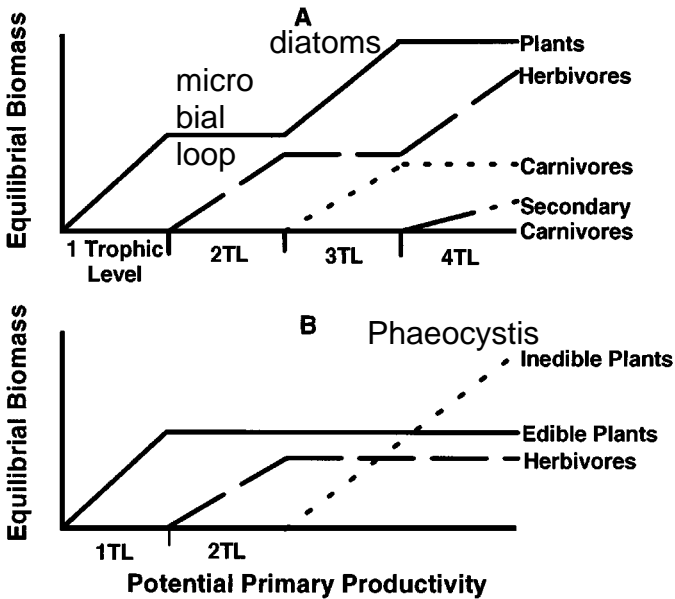
These two contrasting views (bottom-up vs. top-down) make very different predictions about patterns of covariation in biomass at adjacent trophic levels; empirical evidence lends support for both perspectives. A bottom-up approach argues that all trophic levels should increase with productivity. Numerous studies in aquatic systems and some evidence in terrestrial systems show patterns of positive covariation between plant and herbivore biomass, supporting the "bottom-up" perspective. In contrast, much experimental evidence for trophic cascades in enclosure and biomanipulation studies in aquatic systems, and an increasing number of similar studies in terrestrial systems, argue for the "top-down" perspective. Clearly these two forces are not mutually exclusive, and it is evident that the dualism between them is artificial and uninformative. Recent conceptual work has tried to synthesize the two views into one that examines how productivity and predation jointly affect trophic structure (23, 51, 52, 64, 67, 78, 79, 99, 106, 117, 118, 128). Below we summarize the results of these approaches. We then review evidence from both correlational and experimental studies of trophic structure in lake ecosystems, and we identify an important contrast between the results of the two types of studies. We argue that this contrast cannot easily be explained by most current models, and we suggest that a resolution can be found in models that allow for compositional species replacement along environmental gradients. We further argue for the inclusion of species turnover in models by comparing the predictions of such models with other documented patterns in community and ecosystem structure.

### *Simple Theories of Trophic Interactions and Trophic Structure*

Most recent models of trophic structure fall into one of two broad categories. Models that emphasize "vertical structuring" focus on predator-prey interactions and examine the effects of varying the number of trophic levels. This type of model considers communities to be organized as food chains. The second type incorporates "horizontal structuring" in which multiple species at a trophic level compete for resources and share predators.

HSS (54), for example, focused almost exclusively on vertical structuring. They argued that the number of trophic levels present under different conditions influences the pattern of biomass partitioning among trophic levels. They viewed resource limitation and predator limitation as having relatively exclusive roles, predicting that biomass partitioning into trophic levels would

depend on whether there were an even or odd number of trophic levels. Since then (44, 106, 149), these ideas have been modified to account for the joint regulation of organisms by a dynamic balance between predation (and other sources of mortality) and resource competition. This has led to the conclusion that the number of trophic levels (and therefore the importance of trophic cascades) depends on the productivity of the ecosystem. Within the range of conditions in which the number of trophic levels is fixed, adjacent trophic levels respond differently to increasing productivity (i.e. one increases while the other remains constant; see Figure 1A). Despite the conceptual appeal of this



*Figure 1* Biomass accrual of various trophic levels by enhanced ecosystem productivity under different simple models: *A*: Accrual in the simple food chain model developed by Oksanen et al (106). The number of trophic levels present is predicted to increase as shown by four zones on the x-axis. Biomass accrual among organisms at adjacent trophic levels is predicted to be uncorrelated unless the number of trophic levels also changes. Figure modified from Leibold (78). Though nonlinearities may modify these predictions slightly (e.g. 106), most cases result in asymmetric patterns of biomass accrual of organisms at adjacent trophic levels. *B*: Biomass accrual of edible and inedible plants and of herbivores with enhanced ecosystem productivity as developed by Phillips (122). The pattern is similar to that found in the Oksanen model (106) until productivity is high enough that inedible plants invade. Thereafter, enhanced productivity is completely shunted to inedible plants, and edible plants and herbivores are unaffected. Predictions can be modified somewhat by having only partial plant resistance (64, 79), but such cases also result in a strong shunt toward increasingly resistant plants without commensurately large increases in herbivores.

theory, the empirical evidence that the number of trophic levels correlates with productivity, and that biomass responses to productivity depend on the number of trophic levels, remains mixed (10, 20, 35, 94, 100, 123).

In response to HSS (54), several ecologists (39, 102, 169) have emphasized ways in which horizontal structuring that allows compensation among competing species within a trophic level could reduce the importance of top-down regulation of trophic level biomass. For example, when species differ in their vulnerability to consumers, more resistant species can compensate by increasing in abundance when more susceptible species are consumed. Such compensation is still the most common objection to trophic cascades (67, 78, 153). The role of compensatory effects is particularly evident in models in which the bottom-most trophic level is heterogeneous in its edibility and edible plants compete with inedible ones (21, 52, 64, 78, 79, 122). In such cases (Figure 1B), enhanced productivity is less likely to lead to a greater number of trophic levels or to enhanced grazer densities, because the enhanced production primarily benefits the inedible plants.

Both horizontal and vertical factors are critical in determining how trophic structure, and different functional groups within trophic levels (e.g. edible vs inedible plants) respond differently to variation in productivity. Abrams (1) modeled all possible food web configurations involving up to three trophic levels and up to two species per trophic level. He found that different food web configurations resulted in very heterogeneous responses to productivity. The responses were further complicated by nonlinearities in the interactions among species such that very few testable generalizations could be made. Leibold & Wilbur (82) documented qualitatively distinct effects of nutrients on biomass partitioning into trophic levels under different food-web architectures in ponds. More recent, but untested, models have investigated situations in which populations are not at equilibrium and may oscillate or be “chaotic” (4) and when adaptive foraging behavior affects food web interactions (3).

The work on food chains without horizontal structure illustrates one of the important ways that novel large-scale predictions arise when there are vertical compositional changes as well as population or biomass changes in response to bottom-up regulation (106). In models of food chains, correlations between herbivore and plant biomass in response to nutrient levels are explained by variation in the number of trophic levels. However, more subtle but comparable effects can also occur when compositional change occurs within a trophic level (i.e. with horizontal structuring; 79, 122, 156). We argue that these effects are particularly important when there is extensive compositional turnover of species. However, before discussing these models in more detail, we review the experimental and observational literature to highlight discrepancies in our current understanding of top-down and bottom-up regulation of food webs.

### *Incongruences Between Experimental Results and Correlational Studies*

Some limnologists have felt uncomfortable with the dualistic alternation of resource and consumer limitation between adjacent trophic levels suggested by the HSS model, and they have argued more for the bottom-up perspective (99, 173). Support for the importance of resource supply, in contrast with the simple HSS formulation, has arisen from surveys that reveal that plant and herbivore biomass are both positively correlated with eutrophication (increases in nutrient levels in lakes that enhance their productivity) (49, 56, 92, 178). However, the evidence has been largely phenomenological rather than deductive, and correlational data on top-down effects are more difficult to collect (57, 101, 117, 119). Arguments against the importance of trophic cascades and the utility of biomanipulation generally invoke the role of functional heterogeneity among organisms, particularly emphasizing plant compensation (14, 22, 34, 59, 60, 134, 163) but also compensation among animals (25, 40, 72). Changes in phytoplankton composition along a gradient of trophic status are one line of evidence against top-down control (6, 80, 113, 133, 171, 172). Though there is some debate, resistant or toxic algae often increase with eutrophication (134, 111, 172). Similar patterns have been used by terrestrial ecologists to suggest that trophic cascades might be uncommon in terrestrial systems (39, 102, 126, 153). Some researchers have attempted to circumvent this problem at the population level by focusing their analyses on pairwise interactions between herbivores and “edible” plants (93), ignoring the role of “inedible” plants. An important implication of models that include inedible plants is that herbivore populations should not respond strongly to nutrient levels in lakes, but instead, excess nutrients should be sequestered in inedible algae (as shown in Figure 1B). However, experiments reviewed by Leibold (78) and Brett & Goldman (18, 19), and correlational studies such as those of McCauley et al (93), show that herbivores do respond positively to nutrient levels despite the presence of “inedible” algae.

Heterogeneity among herbivores may also limit top-down control. For instance, it has been argued that trophic cascades and successful biomanipulations are more likely in situations in which grazers are dominated by members of the genus *Daphnia*. Several experiments support this claim (78, 144). *Daphnia*'s importance is often explained by its diet breadth and strong population responses. To evaluate the effects on algae, Sarnelle (139) analyzed experiments in which *Daphnia* grazers have been directly or indirectly (via the use of fish predators) manipulated. Using the difference in algal biomass in the two grazer treatments divided by the biomass in the grazer-free treatment (which he named the algal response factor or ARF), he showed that grazers have larger proportional effects on phytoplankton in more eutrophic lakes. Similarly, Mazumder

(88) showed that the regression between algal biomass and total phosphorus levels is different in lakes where *Daphnia* are abundant (which he inferred to indicate food webs with even numbers of “functional” trophic levels) from those where *Daphnia* are rare (which he associated with an odd number of trophic levels). Both of these authors used their evidence to support top-down models of interactions in plankton, especially in eutrophic situations where Carney (22) has argued that “inedible” algae would prevent its occurrence.

Few studies have simultaneously discussed both experimental and correlational evidence for trophic regulation (25, 99), and there has been remarkably little discussion what a lack of congruence between experimental and correlational patterns might imply. McQueen et al (99) compared regressions of trophic level biomasses in surveys related to eutrophication with data from experiments manipulating fish predation, concluding that both top-down and bottom-up processes were important. They further argued that bottom-up effects were likely to be more important because top-down effects tended to “dissipate” as they proceeded to lower and lower trophic levels, particularly at the plant-herbivore interface. This analysis is, however, mostly phenomenological, and it suffers because the contrast between bottom-up and top-down effects is confounded with the type of evidence used (experiments vs surveys) (141).

Carpenter & Kitchell (25) also discussed the relative merits of short-term experiments (usually replicated in relatively small enclosures) with the longer studies involving whole-lake manipulations; they concluded that important additional processes occurring in whole lakes make extrapolation from most experiments difficult because such extrapolations ignore processes that occur on longer and larger scales. They have particularly focused on the roles of horizontal migrations by fishes and the coupling of benthic and pelagic processes.

We argue that differences between experimental and correlational patterns have the potential to be just as informative as similarities in distinguishing among models. Here we explore the contrasts between studies of lake communities that have responded to variation in nutrient levels and predation over long time scales (surveys of lakes that have diverged over tens to hundreds of years), whole-lake experiments (lasting from one to five years), and short-term enclosure experiments (lasting less than one year). Differences between them might inform us about the role of additional long-term, large-scale processes that are absent in the small-scale studies. A direct comparison of three approaches to the same questions allows us to qualitatively evaluate the effects of temporal and spatial scales.

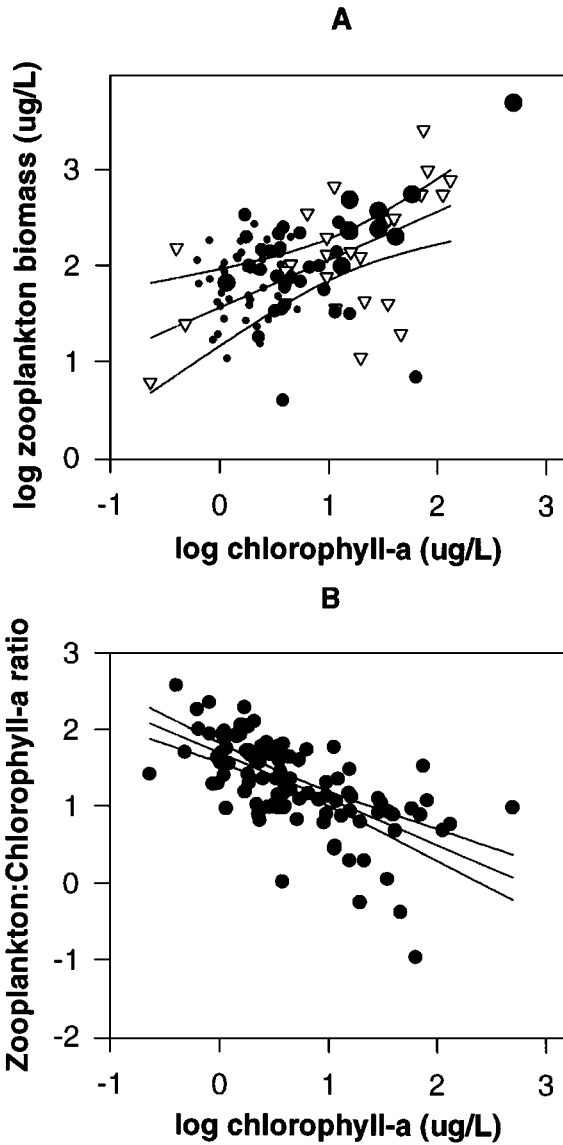
We start by considering large-scale patterns in relation to nutrient levels and predation in lakes. To evaluate the patterns associated with nutrient levels, we focus on survey data. Data such as these have previously been examined by

others (32, 56, 92, 110). We pool data from these and additional studies and present them as a standard by which to evaluate the experimental evidence we discuss below. Because virtually all proponents of trophic cascades in lakes acknowledge the role of nutrients, we also want to evaluate the long-term, whole-lake effects of fish predation on plankton communities in a way that controls (as much as possible) for nutrient levels. The best sources of data to investigate whole-lake responses to predator effects were biomanipulation studies and studies of historical changes in fish predation. We analyzed all studies (starting with those listed in Refs. 13 and 146 and supplemented by a search for more recent studies) that included phytoplankton and herbivore biomass data and, if possible, nutrient data.

Because models make different predictions about the relative responses of plants and herbivores to nutrients, we focus on the relationship between algal biomass (converted to chlorophyll-a concentration) and zooplankton biomass (usually restricted to crustaceans but sometimes including rotifers, converted to dry weight concentration). The data are shown in Figures 2A and 2B. As in previous studies, our compilation shows a strong correlation between algal and zooplankton biomass. These data disagree with the predictions of both of the simplest models of food chains, and of the models incorporating inedible plants described above (Figures 1A and 1B). The pattern is clearly related to variation in nutrient levels and thus substantiates the bottom-up view, suggesting that interactions between resources and their consumers might be “donor-controlled” without feedback from herbivores on plants. At first glance, this pattern tends to be incompatible with the evidence cited above about the role of grazers in lake ecosystems, especially since many of the lakes in the survey contain *Daphnia*, which are often able to control algae (88, 139).

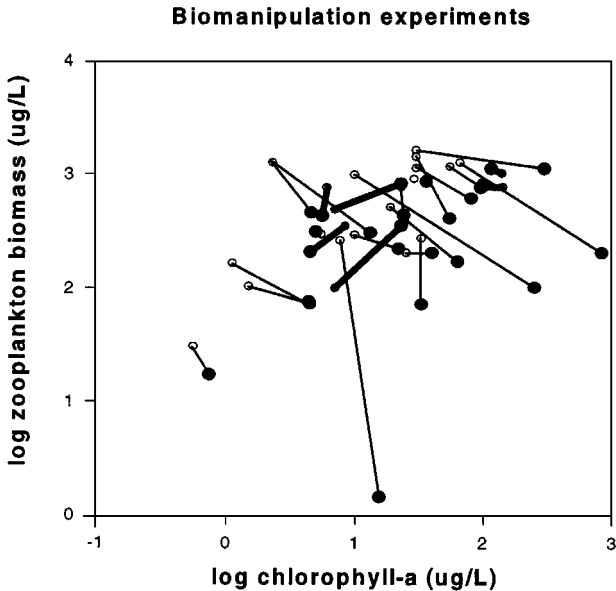
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*Figure 2* Patterns of variation in unmanipulated lakes. *A*: Herbivore biomass (evaluated as log zooplankton biomass) is correlated with plant biomass (evaluated as log chlorophyll-a concentration) in lakes with different total phosphorus levels. The scaling factor (slope of the log-log regression) is 0.404 with a standard error of 0.017; and the correlation coefficient (0.48) is highly significant ( $p < 0.001$ ). Both variables are also strongly correlated with log total phosphorus (TP), indicated by the size of the symbol for each data point. Solid circle size is proportional to logTP, and open triangles denote studies in which data on TP was not available. *B*: Relative partitioning of biomass between zooplankton and algae expressed as the log of the ratio of zooplankton dry weight ( $\mu\text{g/L}$ ) to the log of chlorophyll-a concentration ( $\mu\text{g/L}$ ). Assuming that plant dry weight is about 100 times the chlorophyll concentration (6), these data show that over the three orders of magnitude in chlorophyll-a concentration, the ratio of herbivore to plant biomass declines from roughly equal partitioning between plants and herbivores to a trophic pyramid in which plant biomass is roughly 100-fold higher than herbivore biomass. Data are from References (32, 56, 61, 63, 76, 92, 109, 135, 148, 152, 159).



These data, however, also indicate just how dramatically trophic structure can vary with nutrient levels. The ratio of herbivore to plant biomass in these lakes varies by over two orders of magnitude (Figure 2B) and hints at the huge variability in ecosystem function that must accompany such variation. As in previous studies, the biomass of herbivores declines relative to plants as lakes become more productive, and this again seems superficially inconsistent with claims that grazers (at least *Daphnia*) are more important in eutrophic systems (88, 139).

This positive correlation between plant and herbivore biomass with eutrophication is also evident in the biomanipulation studies (Figure 3). When algal and zooplankton biomass are plotted without regard to fish densities, the data show the same relationship as in the survey studies described above. However, with a few notable exceptions, increases in fish populations within lakes tend



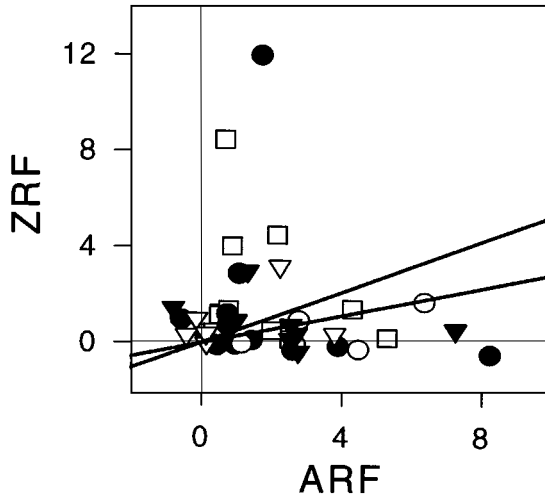
*Figure 3* Effects of biomanipulation on plants and herbivores as measured by log chlorophyll concentration and log zooplankton dry weight from whole-lake experiments. Each line shows the results of a single study in which planktivore densities have been altered. Lines connect low planktivory data (*open circles*) to the high planktivory data (*solid circles*). Most cases (shown with *thinner lines*) point from the upper left to the lower right, indicating a trophic cascade. The six exceptions are illustrated with *thicker lines* and show patterns inconsistent with trophic cascades. Data are from References (15, 16, 25, 37, 47, 71, 84, 98, 120, 132, 138, 150, 151, 161, 168, 162, 170).

to alter trophic structure by decreasing herbivore abundances and increasing plants (i.e. a trophic cascade). Values for pre- and post-manipulated lakes fall mostly within the range of values found in the survey, supporting the view that much of the variation in trophic structure that is not explained by nutrient levels can be attributed to variation in fish predation (23).

Information from these surveys and biomanipulation studies can be supplemented by a growing body of replicated, controlled experiments usually conducted in artificial pond arrays and enclosures. Such experiments have advantages over the survey and unreplicated biomanipulation experiments described above. In particular, the biomanipulation studies have the advantage (and the flaw) that they allow an enormous array of additional processes to influence their outcome, which cannot occur in the smaller enclosures (e.g. whole lake processes, unique historical phenomena, uncontrolled climatic effects). Replicated experiments control for many of these possibilities and allow a more focused understanding of mechanisms behind the results. Here we explore the outcome of food-web interactions when local populations interact on the time scale of weeks to months and are not confounded with some of the longer-time and larger-scale processes, which are not encompassed by the theories described above in which there is no compositional change.

To analyze these data we define a unitless metric, the “zooplankton response factor” (ZRF), analogous to ARF (139). We divide the magnitude of nutrient effects on zooplankton and algae by their densities in the low nutrient treatment. For predator manipulations we standardize zooplankton by their biomass in the low predation treatment and algae by their biomass in the high predation treatment (where the value more likely reflects their “carrying capacity”). The relationship between ARF and ZRF should correspond to the slope of the response on log-log plots of their respective biomasses. This method allows us to compare relative responses without having to account for differences either in the magnitude of the manipulations or in baseline environmental conditions, with expectations from survey patterns.

We analyzed data from published studies that manipulated planktivorous fish or nutrients (nitrogen and/or phosphorus) in mesocosms or artificial experimental ponds, and which reported both phytoplankton and zooplankton standing crops. Multiple comparisons were made both for factorial studies that manipulated both nutrients and predators (for instance, high vs low fish at both high and low nutrients) and for studies with more than two treatment levels. The results of nutrient manipulations show a surprising level of heterogeneity (Figure 4). In some cases, zooplankton responded by increasing much more strongly than algae, whereas in other cases, algae increased much more strongly than zooplankton. Neither extreme responses corresponded with expectations from the survey, which predicted much less asymmetric responses. The 95%



*Figure 4* Responses of plants and herbivores to nutrient additions in replicated enclosure and small pond experiments. The plant response is plotted as the unitless algal response factor (ARF) equal to the difference between the two treatments in some measure of plant biomass (usually chlorophyll-a concentration) divided by the biomass in the low nutrient treatment. The zooplankton response is plotted as the identically defined (using zooplankton biomass instead of algal biomass) zooplankton response factor (ZRF). Shaded symbols denote cases in which *Daphnia* were present, whereas open symbols denote experiments conducted in situations where *Daphnia* were absent. Triangles denote experiments conducted in the presence of fish predators, whereas circles denote experiments conducted in the absence of fish. Open squares denote results of whole-lake manipulations (regardless of *Daphnia* incidence or fish presence). The two lines indicate the joint 95% confidence interval expected if ARF and ZRF resulted from biomass responses observed in the survey data (Figure 2). Responses are significantly more heterogeneous than expected ( $p < 0.001$ ). Data are from References (26, 38, 42, 43, 55, 58, 68, 74, 75, 77, 90, 103, 114, 130, 179).

confidence interval of the slope from the survey relationship of algal and zooplankton biomass, plotted in Figure 4 along with the results of the experiments described above, highlights this dichotomy.

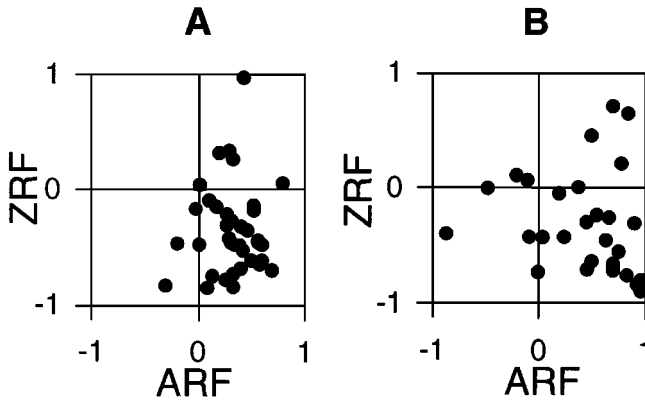
Taken together, these results support the notion that an unknown aspect of each of the local ecosystems (such as the number of trophic levels or some other aspect of food-web architecture) interacts with nutrient enhancement to produce dramatically different results. One possibility is that some of the experiments were conducted in situations with an odd number of functional trophic levels, whereas others were conducted with an even number of trophic levels. Another possibility is that the occurrence of *Daphnia* alters the response to nutrients because it influences the likelihood that some component of the algal community will be inedible. To examine these possibilities, we classified each

study as to whether fish were present in the enclosures and whether *Daphnia* were present in the original zooplankton assemblage. No striking patterns of association emerged between the results and the number of trophic levels or occurrence of *Daphnia* (Figure 4).

We also reviewed the results of whole-lake experimental manipulations of nutrients, often conducted to enhance fish production in otherwise oligotrophic conditions. Figure 4 shows ARFs and ZRFs obtained in these larger-scale and longer-term experiments (usually 1–3 years of monitoring after nutrient additions). The results are as variable as are those of the enclosure studies described above. Toxic effects of nutrients on zooplankton have been invoked in some of the cases in which algal blooms have occurred without corresponding increases in zooplankton (86), but no direct evidence for toxicity was presented. Because most of the effects in which zooplankton responded without similarly large increases in algae occurred in the presence of *Daphnia*, these results tended to reinforce the view that trophic cascades are more important, and donor control less important, in such situations.

Finally, we examined experimental manipulations of fish (“top-down” manipulation) in enclosures and replicate artificial ponds. In order to compare experimental fish manipulations to the whole-lake biomanipulation studies, we calculated the ARF and ZRF (Figures 5A and 5B). Generally, the distribution of results from the enclosures are in good agreement with the biomanipulation studies as indicated by the occurrence of most of the data points in the lower right quadrant. This quadrant corresponds to increased fish predation that leads to a decrease in zooplankton and an increase in algae. Thus, trophic cascades commonly occur, but some noteworthy exceptions involve all three other possible outcomes. In situations in which an increase in fish predation is associated with an increase in zooplankton biomass and a decrease in algae (the upper left quadrant), the effects are small and possibly not significant. However, in some cases increased fish predation results in an increase in zooplankton biomass as well as increased algal biomass (the upper right quadrant), and some studies show both effects were negative (the lower left quadrant). These may reflect cases in which effects were largely mediated through changes in nutrient levels (33, 163, 164) or other unknown indirect pathways. Responses in trophic structure in the enclosure experiments as expressed by the ratio of herbivore to plant biomass were also remarkably similar to the biomanipulation studies, suggesting that most trophic structure responses are not often strongly affected by whole-lake processes, though the literature does document particular instances in which such phenomena occur (25).

In summary, these analyses reveal a striking dichotomy between the responses of trophic structure to experimental nutrient and predator manipulations and variation in trophic structure along natural nutrient gradients in lakes.



*Figure 5* Responses of plants and herbivores to manipulations of fish. *A*: Results of experiments in replicated enclosures and small ponds. ARF and ZRF are defined as in Figure 4 except that the differences between treatments in resulting plant biomass are standardized by the plant biomass observed in the high-planktivore situation (most closely related to maximum algal “carrying capacity”), whereas differences in zooplankton biomass are standardized by the plant biomass observed in the low-planktivore treatment (related to zooplankton “carrying capacity”). Data points in the lower right quadrat (declines in zooplankton associated with increases in algae) are consistent with the trophic cascade. Other points are not, and these indicate mostly either simultaneous increases or decreases in both plants and herbivores. Data are from References (42, 57, 58, 61, 96, 89, 90, 114, 115, 130, 158, 165, 166, 167). *B*: Results of whole-lake biomaniipulation studies plotted identically to panel *A*. Most data are consistent with a trophic cascade (in the lower right quadrat), but some cases also show simultaneous increases or decreases in both. Data are from References (15, 16, 25, 26, 37, 47, 71, 73, 84, 98, 120, 132, 138, 150, 151, 161, 162, 168, 170).

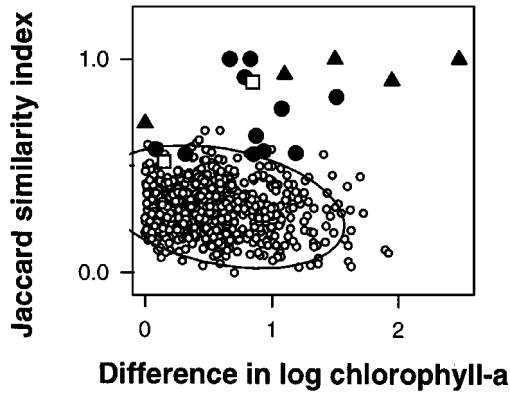
One possibility is that whole-lake processes are absent in small-scale experiments that make them nonrepresentative of natural conditions. However, the observation of similar dichotomous reactions to whole-lake fertilization experiments (Figure 4) argues against the possibility that restricted spatial scale is responsible for the contrast. Further, the similar responses of whole-lake biomaniipulation and small-scale enclosures to manipulations of fish predators also argue that such whole-lake processes, though they may be present, are not sufficiently large to account for the discrepancy.

The occurrence of parallel strong responses by plants and herbivores to nutrients is now understood to be a major line of evidence against simple food chain theories, and other hypotheses have been forwarded to explain this pattern. These explanations have emphasized (*a*) compensation by organisms within trophic levels with different edibilities (52, 78, 153), (*b*) ratio-dependent models in which the functional response of consumers is dependent on the ratio of consumers to resources rather than resource density (9, 46, 62), (*c*) direct

interference among consumers (91, 108, 149, 176), (*d*) nonlinear effects associated with adaptively plastic responses of organisms to predation risk and growth (3), and (*e*) the possibility that non-equilibrium communities will have average patterns that may differ qualitatively from patterns in predicted variation in the equilibrium points (4). Though many of these remain interesting possibilities, compensation (at least among planktonic organisms), ratio-dependence, interference, and nonlinear effects should occur in enclosures as well as in the lakes they supposedly mimic. These models consequently do not adequately explain why patterns among lakes that have diverged over many years differ so much from the results of experiments conducted both in enclosures and on whole-lake ecosystems over shorter periods of time.

Our thesis is that a major shortcoming of the current set of models is the limited extent to which they consider compositional changes within a trophic level. To evaluate whether compositional change along natural gradients was different than that from experiments, we compared the patterns of pairwise similarity in phytoplankton composition among naturally occurring lakes with the average similarity between different treatments in replicated experiments and compositional changes associated with biomanipulation studies. We obtained a matrix of pairwise similarities for an array of 40 lakes along a wide trophic gradient in Florida (155) and related these differences to the pairwise differences in the logarithm of their chlorophyll concentrations. Because our emphasis is on changes associated with the invasion and extinction of species rather than on patterns of relative dominance, we calculated Jaccard coefficients of similarity on the incidence matrix (presence/absence) and ignored changes associated with variation in relative dominance. The data (Figure 6) show that pairwise similarities are generally lower than about 0.5 and that they decrease with increasing differences in levels of eutrophication ( $R = -0.21$ ,  $p < .001$ ). An analysis of a similar gradient in northern fishless ponds (80) shows a very similar pattern.

We compared this distribution with pairwise values obtained from nutrient addition experiments, fish manipulation experiments, and two estimates from biomanipulation experiments that provided data on algal composition with enough resolution to provide useful contrasts with the survey data. Changes in phytoplankton composition resulting from experimental manipulations were substantially less than in the survey and did not show any strong pattern of association with the magnitude of change in plant biomass. This raises the possibility that whatever limits the development of such compositional turnover, especially colonization by species from outside the system, also constrains the responses in trophic structure that we document above. Additional evidence that compositional change is important comes from a mesocosm study (not included in the analyses described above) manipulating nutrients in which initial



*Figure 6* Pairwise similarity (measured using the Jaccard index on dichotomous presence/absence data) in algal composition among lakes (*small open symbols*), enclosure experiments (*solid symbols*), circles denote nutrient addition experiments and triangles denote fish manipulation experiments), and whole lake biomanipulation experiments (*open squares*) in relation to pairwise log-scale differences in mean plant biomass (measured as chlorophyll-a concentration). The data from the experiments (from references (8, 12, 85, 116, 154, 163, 165, 166) are significantly higher than the 95% confidence interval derived from the survey of lakes (155).

phytoplankton and zooplankton diversity was strongly enriched by pooling from numerous ponds with various nutrient levels. This experiment created initial conditions that allowed for species composition to sort out along a nutrient gradient. Roughly parallel responses in algal and zooplankton biomass to nutrients were observed (82). Jaccard similarity of algal composition between low- and high-nutrient treatments in this experiment averaged 0.27, a value akin to the range found in the eutrophic survey shown in Figure 6.

### *Compositional Change and Trophic Structure*

The experimental and observational literature highlights several important discrepancies in our understanding of the regulation of trophic structure by nutrients and predators in lakes. In the first place, results of most experimental work support models that do not allow for compositional change, predicting asymmetric responses by plants and herbivores to eutrophication, whereas correlational analyses suggest roughly proportional increases in both. Secondly, demonstrably less compositional change by algae occurs in experimental enclosures and in whole lake manipulations than in surveys across lakes. These observations imply that compositional change may modify predictions about the regulation of trophic structure from those predicted on the basis of the simpler models described above.

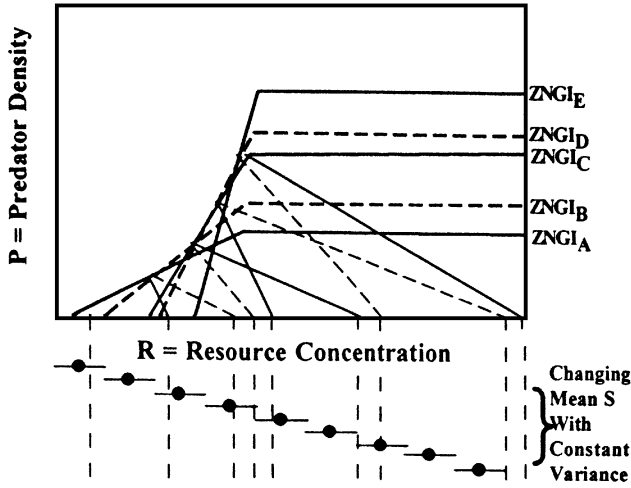
How might this occur? We seek models that allow the simultaneous analysis of biomass responses at all trophic levels, that allow compositional change

within trophic levels, and that function under joint regulation by both predation from above and resource production from below (simultaneous top-down and bottom-up regulation). Simulation models incorporate some of these features (33). However, we focus on simple analytic models in which some species consume and potentially compete for a single resource and are consumed by a single predator (11, 52, 64, 79, 160). Here we concentrate on the analysis of the “keystone predation” model presented by Leibold (79). The model predicts a series of species replacements as the supply of the resource is increased. Greater productivity favors increasingly resistant species, whereas species that are more vulnerable but more efficient at exploiting resources are lost (Figure 7). In this scenario, the trophic structure undergoes small changes as species are replaced along trophic gradients. As in food chain models, the densities of the bottom-most resource and of the predator are enhanced by enhanced nutrient levels, but in addition the intermediate trophic levels are enhanced as well. The community as a whole tracks equilibrium points along a productivity gradient. Species that are good resource competitors but susceptible to predators will dominate at low resource supply rates, whereas highly defended species that are poor resource competitors will replace them as primary productivity increases. The key feature of the model is the “tracking” of a large number of equilibria associated with taxonomic turnover that results in proportional responses by organisms at all three trophic levels.

Clearly, the “keystone predation” model can be only a caricature of the complex array of factors that affect compositional changes because it analyses compositional and trophic structure variation in a guild of species controlled by a single predator and a single resource. Most lakes have, at any time, dozens of planktonic herbivores and dozens to hundreds of plant species. Furthermore, compositional change in both of these groups can be driven by factors other than variation in productivity or top predators per se (including nutrient supply ratios, disturbance, habitat variation, pH, and temperature). There are two ways to interpret patterns of variation in limnetic communities in the context of this model. First, the model might be an adequate descriptor of one subsystem in the more complex array of food web interactions, but this subsystem is strong enough to provide a detectable pattern despite the occurrence of many other complex patterns of interaction. Alternatively, the qualitative predictions made by the model may adequately predict the cumulative behavior of many subsystems that act in parallel but roughly additive ways. Jager et al (70) conducted simulations of more complex food webs (5 species each in 5 trophic levels) in ways that are consistent with the model and found that most of the predictions made by Leibold (79) are obtained even with these additional complexities, supporting the validity of either or both of these interpretations.

Further, because the model assumes that local assemblages track the equilibria along a productivity gradient, it may be that other predictions would hold

A)



B)

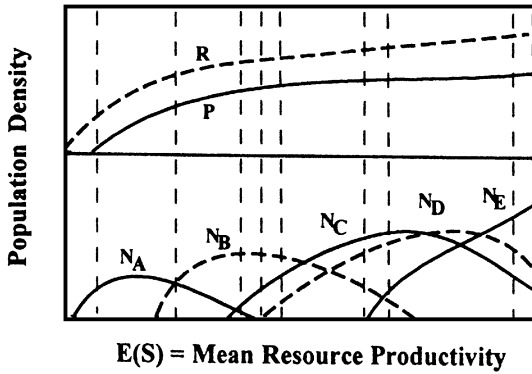


Figure 7 The keystone predator model (64, 79). A: Zero net growth isoclines (labeled “ZNGI<sub>i</sub>” for a group of species ( $i = A-E$ ) that share a common predator (whose density is denoted  $P$ ) and a common resource (with density  $R$ ). The species show a trade-off between exploitation ability (minimum resource requirements in the absence of predators) and their susceptibility to predators (the slope of the ZNGI). For each of the pairwise equilibria that denote coexistence of uninvadable pairs, extensions of the two species’ “impact vectors” are denoted that identify what level of ecosystem productivity will allow each equilibrium. B: Predicted qualitative patterns of densities of predators ( $P$ ), resource levels ( $R$ ), and densities of species  $A-E$  whose ZNGIs are shown in panel A. In a situation with local spatiotemporal variability (denoted by *dots with lines across them* denoting the mean and variance of such variability), both predator and resource densities increase monotonically. Additionally, there is a gradient of species replacements with increasing summed densities of the intermediate group of species. These species consist of good resource exploiters (e.g. species “A”) at low productivity and predator-resistant species (species “E”) at high productivity. Figure is from Leibold (79) who describes the model in detail.

under non-equilibrium situations. We would seek models that investigate trophic structure dynamics under conditions in which local population dynamics and invasion-colonization dynamics are both non-equilibrial. We know of no such models relevant to this situation but anticipate that they will provide additional insights into problems associated with the responses of ecosystems at different time scales. However, we believe the predictions made with the assumptions of equilibrium can serve as a useful starting point for such investigations.

### *Associations with other Community and Ecosystem Attributes*

Because the keystone predation model includes predictions about both the horizontal and vertical structure of food webs, it can also make other predictions about community structure along productivity gradients and link them to predictions that strictly involve trophic structure. These predictions, developed by Holt et al (64), Grover (51, 52), and Leibold (79) and supported by the simulations of Jager et al (70), include the following:

1. *A unimodal relation between species richness within a trophic level and the rate of supply of resources to that trophic level.* In lakes, both algal diversity (5, 80, 105, 129) and zooplankton diversity (36, 80) are unimodally related to various measures of eutrophication (especially to ambient TP levels).
2. *A series of species replacements along a productivity gradient.* Alternative models of biodiversity can predict that even with a unimodal diversity curve as described above, species distribution patterns should consist of nested subsets rather than a series of species replacements. The intermediate peak occurs via the addition of specialists to otherwise less diverse communities dominated by generalists that occur at low and at high productivity (137, 156). Leibold (80) presented an analysis that supports the conclusion that species show replacements rather than nestedness along a productivity gradient in ponds.
3. *Dominance shifts from good resource-exploiters at low productivity to predation-tolerant species at high productivity.* Such predictions are relatively hard to verify because there are relatively few data to link these traits to the wide array of species found along limnetic productivity gradients. In general, however, it is recognized that resistant (or "inedible") algae dominate at higher productivity (80, 81, 171, 172).

Further work on the model of keystone predation involving the effects of compositional turnover may also generate further predictions. For example,

McPeck (95) has used this model to explain patterns of species distributions involving habitat generalists and specialists. Additionally, Grover (51) has examined how such a model acts to determine the “community assembly” process of diversification in local assemblages.

The predictions generated by the keystone predator model are testable and in many cases contrast with the predictions of other models. If our understanding of the various possibilities is sufficiently well developed, it may even be possible to conduct such comparative studies to identify and test alternative models. Leibold (80) conducted a correlative approach to argue that the keystone predation hypothesis is better able to explain variation in community structure in fishless ponds than the “paradox of enrichment” (136), resource heterogeneity (156), or resource ratio (156, 157) hypotheses. Such comparative approaches based on a method of strong inference (125) can strongly complement experimental approaches.

### *Conclusions*

The relative roles of resources and predators in communities and ecosystems are themes that run deep in both ecology and limnology (29, 31, 41, 45, 50, 83, 104, 112). Many simplifying approaches have been taken to discern patterns in the “entangled bank” that results from the joint action of these two processes. Ideas about the regulation of trophic structure of ecosystems provide a fascinating example of how such ideas develop and become progressively more sophisticated as the demands for generality, rigor, and precision have increased. For example, we can trace ideas about the importance of predators from the HSS (54) hypothesis, which was aimed primarily at explaining why plants were common in terrestrial systems (i.e. why the “world was green” rather than “brown”), to Fretwell’s (44) and Oksanen et al’s (106) more sophisticated models that recognized that the productivity of the ecosystem might influence the number of trophic levels and thus explain variation in plant biomass across habitat gradients (i.e. why eastern US grasslands are “greener” than western ones). Subsequently, we can identify trophic models to explain residual variation in nutrient biomass relations (23), as well as models that include variation in plant edibility (52, 78, 122). These more refined models helped to account for variation in plant biomass in the absence of information about the number of trophic levels present. They also predict well the visible patterns in compositional change within trophic levels along productivity gradients (e.g. plant communities). Our goal in this paper is to argue that changes in species composition drive ecosystem-level patterns rather than simply functioning as a by-product of such patterns.

Other approaches have tried to circumvent developing such increasingly sophisticated models. For example, “ratio-dependent models” (in which

functional responses of consumers are determined by the ratio of resource to consumer densities) have been proposed as alternatives to the prey-dependent models (in which functional responses are determined only by the density of the resource) we have emphasized here. Though there is much disagreement about their overall validity (2, 48, 107, 140), ratio-dependent models might be most useful as simplifications of the more complex mechanisms (7, 17). This simplification, however, cannot facilitate our understanding of the association between community and trophic structure that is the focus of this paper. Alternatively, others have advocated approaches that completely ignore mechanisms of population regulation processes in favor of “brute force” empirically predictive methods (121). This approach embodies a sense that ecosystems are too complex to “un-entangle.” We realize that shortcomings in the more realistic, but still somewhat simplistic, models we advocate, such as the keystone predation model, will likely become evident. However, we believe that much of the evidence from the study of trophic structure in lakes and ponds supports many of these predictions, and we suggest that such approaches may be a useful standard for future model development and elaboration.

Trophic cascades have been documented in nonlimnetic ecosystems (e.g. 87, 127, 177). Terrestrial ecosystems also show patterns of biomass accrual similar to those in limnetic systems (30, 94, 100). Trophic interactions in some of these biomes also frequently involve compositional change (e.g. 27, 143). These and other lines of evidence suggest that trophic structure in other ecosystems may be regulated by the same basic processes that seem to work in lakes and ponds (but see 53).

An important aspect of the keystone predator model (and related models) is its ability to synthesize the effects of both “vertical” and “horizontal” structuring as documented in numerous food web studies (28, 123, 124). This synthesis of competitive and predator-prey interrelations is particularly appealing because it begins to provide better links between community and ecosystem approaches (including both the process-oriented, and currently mostly experimental, approaches, as well as the more descriptive “faunistic” or “floristic” approach that describes variation in biotas with environmental gradients). Our recent insights into the community-dependent structure of lake ecosystems, as exemplified by the work surveyed from the experimental, whole-lake biomaniipulation and comparative approaches, suggest the importance of striving for better understanding of the links between these currently disparate approaches.

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