

# SPECIES TURNOVER AND THE REGULATION OF TROPHIC STRUCTURE

*Mathew A. Leibold, Jonathan M. Chase, Jonathan B. Shurin,  
and Amy L. Downing*

Department of Ecology and Evolution, University of Chicago, Chicago,  
Illinois 60637; e-mail: mleibold@pondside.uchicago.edu

**KEY WORDS:** top-down vs bottom-up, biomanipulation, productivity, trophic cascade,  
compositional change

---

## 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.

---

### *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.

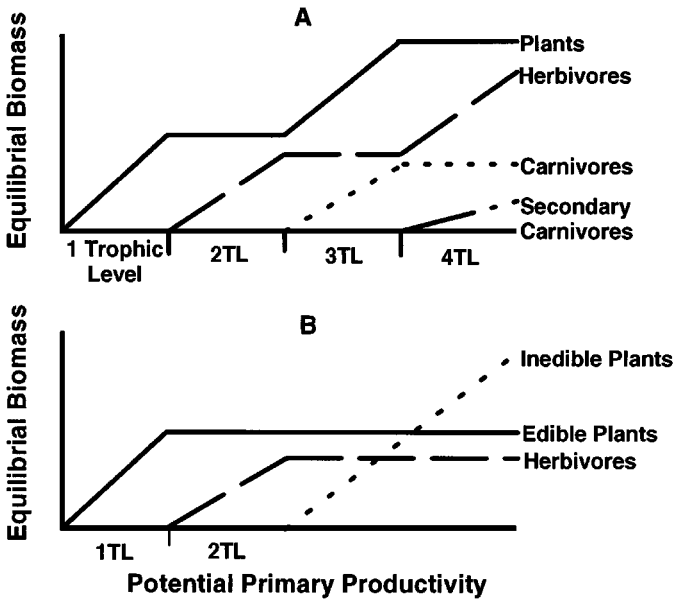
These two contrasting views (bottom-up vs. top-down) make very different predictions about patterns of covariation in biomass at adjacent trophic levels; empirical evidence lends support for both perspectives. A bottom-up approach argues that all trophic levels should increase with productivity. Numerous 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.

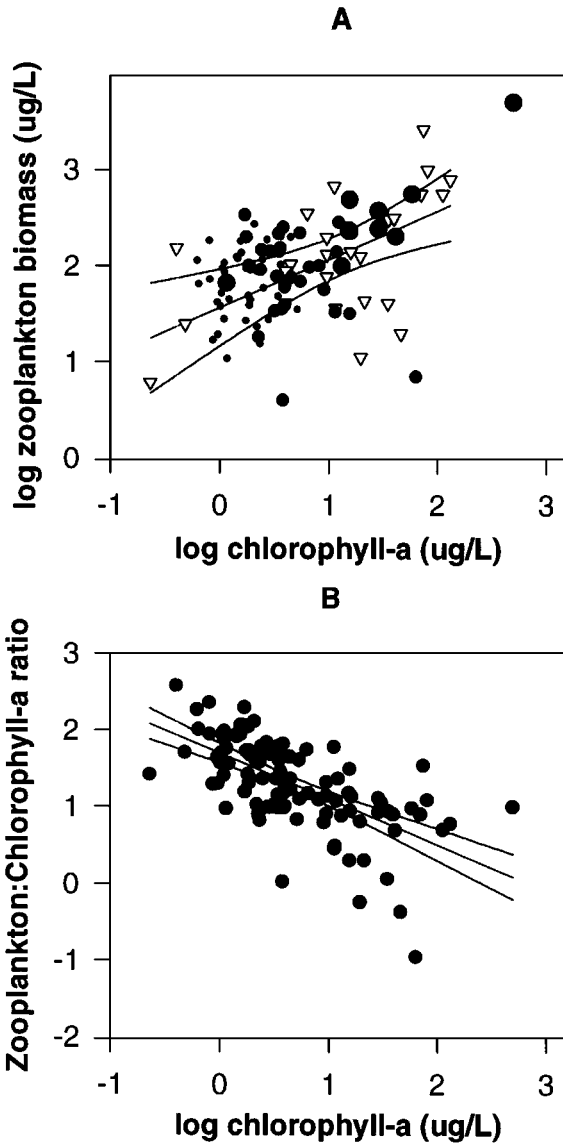
We start by considering large-scale patterns in relation to nutrient levels and predation in lakes. To evaluate the patterns associated with nutrient levels, we focus on survey data. Data such as these have previously been examined by

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).

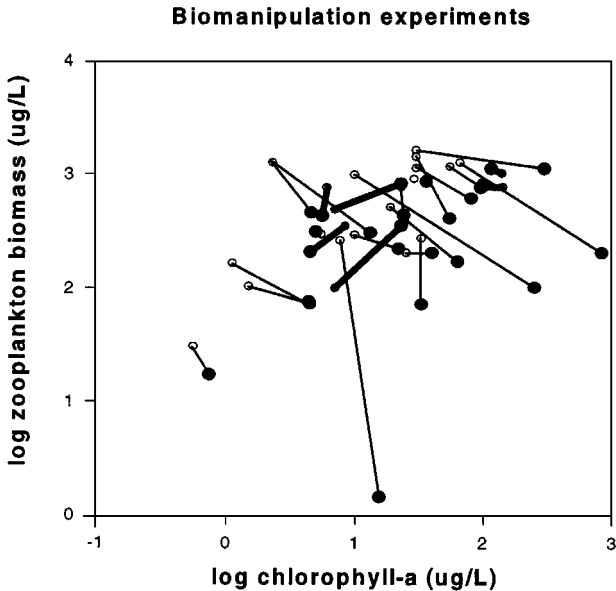
---

*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



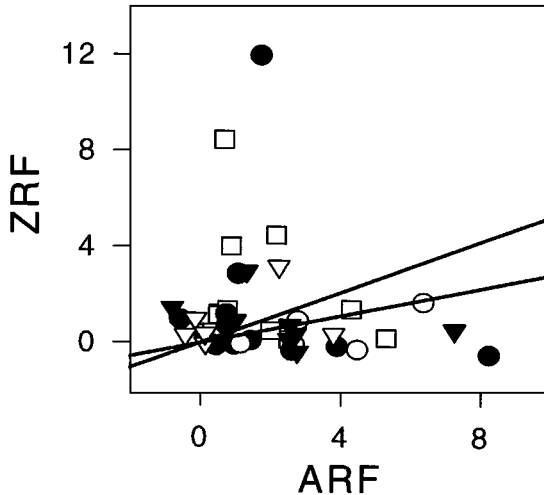
*Figure 3* Effects of biomanipulation on plants and herbivores as measured by log chlorophyll concentration and log zooplankton dry weight from whole-lake experiments. Each line shows the results of a single study in which planktivore densities have been altered. Lines connect low planktivory data (*open 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.

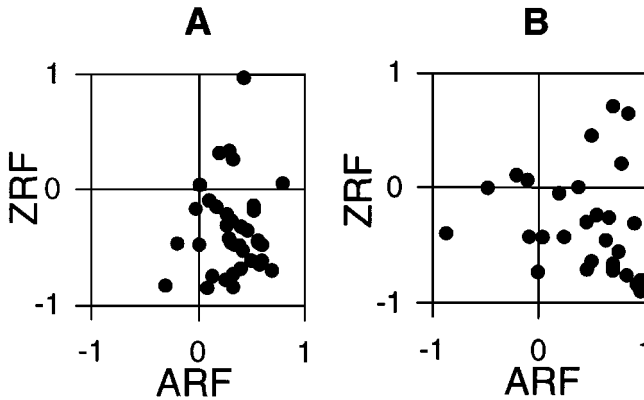
Taken together, these results support the notion that an unknown aspect of each of the local ecosystems (such as the number of trophic levels or some other aspect of food-web architecture) interacts with nutrient enhancement to produce dramatically different results. One possibility is that some of the 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).

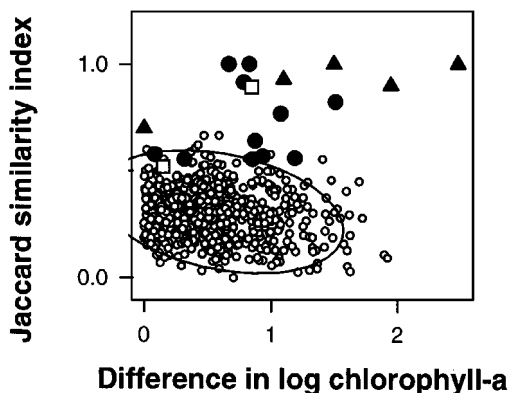
One possibility is that whole-lake processes are absent in small-scale experiments that make them nonrepresentative of natural conditions. However, the observation of similar dichotomous reactions to whole-lake fertilization experiments (Figure 4) argues against the possibility that restricted spatial 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.

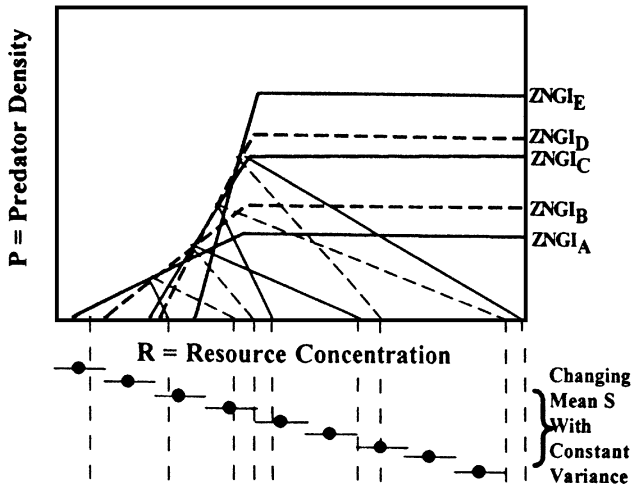
How might this occur? We seek models that allow the simultaneous analysis of biomass responses at all trophic levels, that allow compositional change

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)

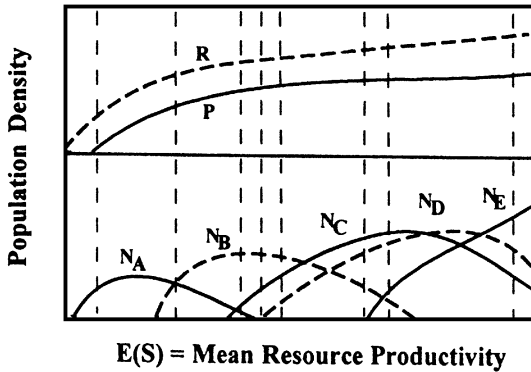


Figure 7 The keystone predator model (64, 79). A: Zero net growth isoclines (labeled “ZNGI<sub>i</sub>” for a group of species ( $i = A-E$ ) that share a common predator (whose density is denoted  $P$ ) and a common resource (with density  $R$ ). The species show a trade-off between exploitation ability (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.

#### ACKNOWLEDGMENTS

We thank Tom Miller, Jean Tsao, Tim Wootton, and an anonymous reviewer for helpful comments on the manuscript and Paul del Giorgio for supplying data. MAL was supported by NSF grants BSR-8817806 and DEB-9509004.

JMC, JBS, and ALD were supported by GAANN fellowships from the US Department of Education.

Visit the *Annual Reviews* home page at  
<http://www.annurev.org>.

#### Literature Cited

1. Abrams PA. 1993. Effects of increased productivity on the abundances of trophic levels. *Am. Nat.* 141:351–71
2. Abrams PA. 1994. The fallacies of “ratio-dependent” predation. *Ecology* 75:1842–50
3. Abrams PA. 1996. Dynamics and interactions in food webs with adaptive foragers. In *Food Webs: Integration of Patterns and Dynamics*, ed. GA Polis, KO Winemiller, pp. 113–21. London/New York: Chapman & Hall
4. Abrams PA, Roth JD. 1994. The effects of enrichment on three-species food chains with nonlinear functional responses. *Ecology* 75:1118–30
5. Agusti S, Duarte CM, Canfield DE. 1991. Biomass partitioning in Florida phytoplankton communities. *J. Plankton Res.* 13:239–45
6. Ahlgren G. 1970. Limnological studies of Lake Norrviken, a eutrophied Swedish lake. *Schwei. Zeitsch. Hydrol.* 32:353–96
7. Akçakaya HR, Arditi R, Ginzburg LR. 1995. Ratio-dependent predation: an abstraction that works. *Ecology* 6:995–1004
8. Andersson G, Berggren H, Cronberg G, Gelin C. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. *Hydrobiologia* 59:9–15
9. Arditi R, Ginzburg LR. 1989. Coupling in predator-prey dynamics: ratio-dependence. *J. Theor. Biol.* 139:311–26
10. Arditi R, Ginzburg LR, Akçakaya HR. 1991. Variation in plankton densities among lakes: a case for ratio-dependent population models. *Am. Nat.* 138:1287–96
11. Armstrong RA. 1979. Prey species replacement along a gradient of nutrient enrichment: a graphical approach. *Ecology* 60:76–84
12. Beklioglu M, Moss B. 1996. Mesocosm experiments on the interaction of sediment influence, fish predation and aquatic plants with the structure of phytoplankton and zooplankton communities. *Freshwater Biol.* 36:315–25
13. Benndorf J. 1990. Conditions of effective biomanipulation; conclusions derived from whole-lake experiments in Europe. *Hydrobiologia* 200/201:187–203
14. Benndorf J. 1995. Possibilities and limits for controlling eutrophication by biomanipulation. *Int. Rev. Gesamten Hydrobiol.* 80:519–34
15. Benndorf J, Kneschke H, Kossatz K, Penz E. 1984. Manipulation of the pelagic food web by stocking with predacious fishes. *Int. Rev. Gesamten Hydrobiol.* 69:407–28
16. Benndorf J, Schultz H, Benndorf A, Unger R, Penz E, et al. 1988. Food-web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen reservoir. *Limnologia* 19:97–110
17. Berryman AA, Gutierrez AP, Arditi R. 1995. Credible, parsimonious and useful predator-prey models—a reply to Abrams, Gleeson and Sarnelle. *Ecology* 76:1980–85
18. Brett MT, Goldman CR. 1996. A meta-analysis of the freshwater trophic cascade. *Proc. Natl. Acad. Sci. USA* 93:7723–26
19. Brett MT, Goldman CR. 1996. Consumer versus resource control in freshwater pelagic food webs. *Science* 275:384–86
20. Briand F, Cohen JE. 1987. Environmental correlates of food chain length. *Science* 238:956–60
21. Briand F, McCauley E. 1978. Cybernetic mechanisms in lake plankton systems: how to control undesirable algae. *Nature* 273:228–30
22. Carney HJ. 1990. A general hypothesis for the strength of food web interactions in relation to trophic state. *Int. Ver. Theor. Angew. Limnol. Verh.* 24:487–92
23. Carpenter SR, Kitchell JF. 1984. Plankton community structure and limnetic primary production. *Am. Nat.* 124:159–72
24. Deleted in proof
25. Carpenter SR, Kitchell JF. 1993. *The Trophic Cascade in Lakes*. Cambridge, UK: Cambridge Univ. Press. 385 pp.

26. Carpenter SR, Kitchell JF, Cottingham KL, Schindler DE, Christensen DL, et al. 1996. Chlorophyll variability, nutrient input, and grazing: evidence from whole-lake experiments. *Ecology* 77:725–35
27. Chase JM. 1997. Effects of a central place forager on food chain dynamics and spatial pattern in meadows. *Ecology*. In press
28. Cohen JE, Briand F, Newman CM. 1990. *Community Food Webs: Data and Theory*. New York: Springer-Verlag
29. Connell J. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–23
30. Cyr H, Pace ML. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *Nature* 361:148–50
31. Darwin CR. 1859. *The Origin of Species*. Reprinted 1976. New York: Macmillan
32. del Giorgio PA, Gasol JM. 1995. Biomass distribution in freshwater plankton communities. *Am. Nat.* 146:135–52
33. DeAngelis DL. 1992. *Dynamics of Nutrient Cycling and Food Webs*. New York/London: Chapman & Hall
34. DeMelo R, France R, McQueen DJ. 1992. Biomanipulation: hit or myth. *Limnol. Oceanogr.* 37:192–207
35. Diehl S, Lundberg PA, Gardfjell H, Oksanen L, Persson L. 1993. Daphnia-phytoplankton interactions in lakes: Is there a need for ratio-dependent consumer-resource models? *Am. Nat.* 142:1052–61
36. Dodson SI. 1991. Species richness of crustacean zooplankton in European lakes of different sizes. *Int. Ver. Theor. Angew. Limnol. Verh.* 24:1223–29
37. Duncan A. 1990. A review: limnological management and biomanipulation in the London reservoirs. *Hydrobiologia* 200/201:541–48
38. Edmonson WT, Litt AH. 1982. Daphnia in Lake Washington. *Limnol. Oceanogr.* 27:272–93
39. Ehrlich PR, Birch LC. 1967. The “balance of nature” and “population control”. *Am. Nat.* 101:97–107
40. Elser JJ, Luecke C, Brett MT, Goldman CR. 1995. Effects of food web compensation after manipulation of a rainbow trout in an oligotrophic lake. *Ecology* 76:52–69
41. Elton C. 1927. *Animal Ecology*. London: Sidgwick & Jackson
42. Faafeng BA, Hessen DO, Brabrand A, Nilssen JP. 1990. Biomanipulation and food-web dynamics—the importance of seasonal stability. *Hydrobiologia* 200/201:119–28
43. Findlay DL, Kasian SEM. 1987. Phytoplankton community responses to nutrient addition in lake 226, Experimental Lakes Area, Northwestern Ontario. *Can. J. Fish. Aquat. Sci.* 44:35–46 (Suppl.)
44. Fretwell SD. 1977. The regulation of plant communities by food chains exploiting them. *Perspect. Biol. Med.* 20:169–85
45. Gause GF. 1934. *The Struggle for Existence*. New York: Hafner
46. Getz WM. 1984. Population dynamics: a per capita resource approach. *J. Theor. Biol.* 108:623–43
47. Giussani G, de Bernardi R, Ruffoni T. 1990. Three years experience in biomanipulating a small eutrophic lake: Lago di Candia (Northern Italy). *Hydrobiologia* 200/201:357–66
48. Gleeson SK. 1994. Density dependence is better than ratio dependence. *Ecology* 75:1834–35
49. Gliwicz ZM. 1975. Effect of zooplankton grazing on photosynthetic activity and composition of phytoplankton. *Int. Ver. Theor. Angew. Limnol. Verh.* 19:1490–97
50. Grinnell J. 1917. The niche-relationships of the California Thrasher. *The Auk* 34:427–33
51. Grover JP. 1994. Assembly rules for communities of nutrient limited plants and specialist herbivores. *Am. Nat.* 94:421–25
52. Grover JP. 1995. Competition, herbivory, and enrichment: nutrient-based models for edible and inedible plants. *Am. Nat.* 145:746–74
53. Hairston NG Jr, Hairston NG Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *Am. Nat.* 142:379–411
54. Hairston NG, Smith FE, Slobodkin LB. 1960. Community structure, population control, and competition. *Am. Nat.* 44:421–25
55. Hall DJ, Cooper WE, Werner EE. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* 15:839–928
56. Hanson JM, Peters RH. 1984. Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. *Can. J. Fish. Aquat. Sci.* 41:439–45
57. Hansson L-A. 1992. The role of food chain composition and nutrient availability in shaping algal biomass development. *Ecology* 73:241–47
58. Hansson L-A, Carpenter SR. 1993. Relative importance of nutrient availability and food chain for size and community composition in phytoplankton. *Oikos* 67:257–63

59. Harris GP. 1986. *Phytoplankton Ecology: Structure, Function and Fluctuation*. Cambridge, UK: Cambridge Univ. Press
60. Harris GP. 1994. Pattern, process, and prediction in aquatic ecology—a limnological view of some general ecological problems. *Freshwater Biol.* 32:143–60.
61. Havens KE. 1993. Responses to experimental fish manipulations in a shallow, hypereutrophic lake: the relative importance of benthic nutrient recycling and trophic cascade. *Hydrobiologia* 254:73–80
62. Herendeen RA. 1995. A unified quantitative approach to trophic cascade and bottom-up: top-down hypotheses. *J. Theor. Biol.* 176:13–26
63. Hessen DO, Andersen T, Lyche A. 1990. Carbon metabolism in a humic lake: pool sizes and cycling through zooplankton. *Limnol. Oceanogr.* 35:84–99
64. Holt RD, Grover J, Tilman D. 1994. Simple rules for interspecific dominance in systems with exploitation and apparent competition. *Am. Nat.* 144:741–71
65. Hrbacek J, Dvorakova M, Korinek V, Prochazkova L. 1961. Demonstration of the effects of fish stock on the species composition of zooplankton and the intensity of the metabolism of the whole plankton association. *Ver. Theor. Angew. Limnol. Verh.* 14:192–95
66. Huismann J, Weissing FJ. 1995. Competition for nutrients and light in a mixed water column: a theoretical analysis. *Am. Nat.* 146:536–64
67. Hunter MD, Price PW. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–32
68. Hyatt KD, Stockner JG. 1985. Response of Sockeye Salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. *Can J. Fish. Aquat. Sci.* 42:320–31
69. Deleted in proof
70. Jager HI, Gardner RH, DeAngelis DL, Post WM. 1984. *A simulation approach to understanding the processes that structure food webs*. ORNL/TM-8904. Oak Ridge, TN: Oak Ridge National Laboratory 171 pp.
71. Jeppesen E, Sondergaard M, Mortensen E, Kristensen P, Riemann B, et al. 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic temperate lakes 1: cross-analysis of three Danish case-studies. *Hydrobiologia* 200/201:205–8
72. Kerfoot WC, DeMott WR. 1984. Food web dynamics: dependent chains and vaulting. In *Trophic Interactions within Aquatic Ecosystems*, ed. DG Meyers, JR Strickler, pp. 347–381. Washington, DC: Westview
73. Langeland A. 1990. Biomannipulation in Norway. *Hydrobiologia* 200/201:535–40
74. Langeland A, Reinertsen H. 1982. Interaction between phytoplankton and zooplankton in a fertilized lake. *Holarct. Ecol.* 5:253–72
75. Larocque I, Mazumder A, Proulx M, Lean DRS, Pick FR. 1996. Sedimentation of algae: relationships with biomass and size distribution. *Can. J. Fish. Aquat. Sci.* 53:1133–42
76. Lean DRS, Fricker HJ, Charlton MN, Cuhel RL, Pick FR. 1987. The Lake Ontario life support system. *Can. J. Fish. Aquat. Sci.* 44:2230–40
77. LeBrasseur RJ, McAllister CD, Barraclough WE, Kennedy OD, Manzee J, et al. 1978. Enhancement of Sockeye Salmon (*Oncorhynchus nerka*) by lake fertilization in Great Central Lake: summary report. *J. Fish. Res. Board Can.* 35:1580–96
78. Leibold MA. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am. Nat.* 134:922–49
79. Leibold MA. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. *Am. Nat.* 147:784–812
80. Leibold MA. 1997. Biodiversity and nutrient enrichment in pond plankton communities. *Evol. Ecol.* In press
81. Leibold MA. 1997. Do competition models predict nutrient availabilities in limnetic ecosystems? *Oecologia* 110:132–42
82. Leibold MA, Wilbur HM. 1992. Interactions between food-web structure and nutrients on pond organisms. *Nature* 360:341–43
83. Lindeman RL. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399–418
84. Lyche A, Faafeng BJ, Brabrand A. 1990. Predictability and possible mechanisms of plankton response to reduction of planktivorous fish. *Hydrobiologia* 200/201:251–61
85. Lynch M, Shapiro J. 1981. Predation, enrichment, and phytoplankton community structure. *Limnol. Oceanogr.* 26:86–102

86. Malley DF, Chang PSS, Findlay DL, Linsey GA. 1988. Extreme perturbation of the zooplankton community of a small precambrian shield lake by the addition of nutrients. *Verh. Int. Verein. Limnol.* 23:2237–47
87. Marquis RJ, Whelan CJ. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75:2007–14
88. Mazumder A. 1994. Patterns of algal biomass in dominant odd- vs. even-link lake ecosystems. *Ecology* 75:1141–49
89. Mazumder A, Lean DRS. 1994. Consumer-dependent responses of lake ecosystems to nutrient loading. *J. Plankton Res.* 16:1567–80
90. Mazumder A, Taylor WD, Lean DRS, McQueen DJ. 1992. Partitioning and fluxes of phosphorus: mechanisms regulating the size-distribution and biomass of plankton. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 35:121–43
91. McCarthy MA, Ginzburg LR, Akakaya HR. 1995. Predator interference across trophic chains. *Ecology* 76:1310–19
92. McCauley E, Kalff J. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. *Can. J. Fish. Aquat. Sci.* 38:458–63
93. McCauley E, Murdoch WW, Watson S. 1988. Simple models and variation in plankton densities among lakes. *Am. Nat.* 132:383–403
94. McNaughton SJ, Oesterheld M, Frank DA, Williams KJ. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial grasslands. *Nature* 341:142–144
95. McPeck MA. 1996. Trade-offs, food web structure, and the coexistence of habitat specialists and generalists. *Am. Nat.* 148:S124–38 (Suppl.)
96. McQueen DJ, Post JR. 1985. Enclosure experiments: the effects of planktivorous fish. *Lake and Reservoir Management, EPA Doc. EP8.2-L14/1985*, pp. 313–318. Washington, DC: USGPO
97. McQueen DJ, France R, Kraft C. 1992. Confounded impacts of planktivorous fish on freshwater biomanipulations. *Arch. Hydrobiol.* 125:1–24
98. McQueen DJ, Johannes MRS, Post JR, Stewart TJ, Lean DRS. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol. Monogr.* 59:289–309
99. McQueen DJ, Post JR, Mills E. 1986. Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.* 43:1571–1581
100. Moen J, Oksanen L. 1991. Ecosystem trends. *Nature* 353:510
101. Moss B, McGowan S, Carvalho L. 1994. Determination of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland meres. *Limnol. Oceanogr.* 39:1020–29
102. Murdoch WW. 1966. "Community structure, population control, and competition": a critique. *Am. Nat.* 100:219–26
103. O'Brien WJ, deNoyelles F Jr. 1974. Relationship between nutrient concentration, phytoplankton density, and zooplankton density in nutrient enriched experimental ponds. *Hydrobiologia* 44:105–25
104. Odum EP. 1971. *Fundamentals of Ecology*. Philadelphia: Saunders. 3rd ed.
105. Ogawa Y, Ichimura S. 1984. Phytoplankton diversity in inland waters of different trophic status. *Jpn. J. Limnol.* 45:173–77
106. Oksanen L, Fretwell SD, Arrüda J, Miemela P. 1981. Exploitation ecosystems along gradients of primary productivity. *Am. Nat.* 118:240–61
107. Oksanen L, Moen J, Lundberg PA. 1992. The time-scale problem in exploiter-victim models: Does the solution lie in ratio-dependent exploitation? *Am. Nat.* 140:938–960
108. Oksanen T, Power ME, Oksanen L. 1995. Ideal free habitat selection and consumer-resource dynamics. *Am. Nat.* 146:565–85
109. Pace ML. 1984. Zooplankton community structure, but not biomass, influences the phosphorus-chlorophyll a relationship. *Can. J. Fish. Aquat. Sci.* 41:1089–96
110. Pace ML. 1986. An empirical analysis of zooplankton community size structure across lake trophic gradients. *Limnol. Oceanogr.* 31:45–55
111. Paerl HW. 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnol. Oceanogr.* 33:823–47
112. Paine RT. 1966. Food web complexity and species diversity. *Am. Nat.* 100:65–75
113. Palmer CM. 1959. *Algae in water supplies. An illustrated manual on the identification, significance, and control of algae in water supplies.* US Dept. Public Health Service. Cincinnati, OH: Taft Sanitary Engin. Ctr.
114. Pérez-Fuentetaja A, McQueen DJ, Demers E. 1996. Stability of oligotrophic and eutrophic planktonic communities after disturbance by fish. *Oikos* 75:98–110
115. Pérez-Fuentetaja A, McQueen DJ, Ramcharan CW. 1996. Predator-induced

- bottom-up effects in oligotrophic systems. *Hydrobiologia* 317:163–176
116. Pérez-Martínez C, Cruz-Pizarro L. 1995. Species-specific phytoplankton responses to nutrients and zooplankton manipulations in enclosure experiments. *Freshwater Biol.* 33:193–203
  117. Persson L, Andersson G, Hamrin SF, Johansson L. 1988. Predator regulation and primary production along the productivity gradient. In *Complex Interactions in Lake Communities*, ed. SR Carpenter, pp. 45–68. New York: Springer-Verlag
  118. Persson L, Bengtsson J, Menge BA, Power ME. 1996. Productivity and consumer relations—concepts, patterns and mechanisms. In *Food Webs: Integration of Patterns and Dynamics*, ed. GA Polis, KO Winnemiller, pp. 396–434. London/New York: Chapman and Hall
  119. Persson L, Diehl S, Johansson L, Andersson G, Hamrin SF. 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. *Am. Nat.* 140:59–84
  120. Persson L, Johansson L, Andersson G, Diehl S, Hamrin SF. 1993. Density-dependent interactions in lake ecosystems: whole lake perturbation experiments. *Oikos* 66:193–208
  121. Peters RH. 1986. The role of predation in limnology. *Limnol. Oceanol.* 31:1143–59
  122. Phillips OM. 1974. The equilibrium and stability of simple marine systems. II. Herbivores. *Arch. Hydrobiol.* 73:310–33
  123. Pimm SL. 1982. *Food Webs*. London: Chapman & Hall
  124. Pimm SL. 1991. *The Balance of Nature?* Chicago, IL: Univ. Chicago Press
  125. Platt JR. 1964. Strong inference. *Science* 146:347–53
  126. Polis GA, Strong DR. 1996. Food web complexity and community dynamics. *Am. Nat.* 147:813–846
  127. Power ME. 1990. Effects of fish in river food webs. *Science* 250:811–814
  128. Power ME. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology* 73:733–746
  129. Proulx M, Pick FR, Mazumder A, Hamilton PB, Lean DRS. 1996. Experimental evidence for interactive impacts of human activities on lake algal species richness. *Oikos* 76:191–95
  130. Proulx M, Pick FR, Mazumder A, Hamilton PB, Lean DRS. 1996. Effects of nutrients and planktivorous fish on the phytoplankton of shallow and deep aquatic systems. *Ecology* 77:1556–1572
  131. Deleted in proof
  132. Reinertsen H, Jensen A, Koksvik JI, Langeland A, Olsen Y. 1990. Effects of fish removal on the limnetic ecosystem of a eutrophic lake. *Can. J. Fish. Aquat. Sci.* 47:166–73
  133. Reynolds CS. 1984. The ecological basis for the successful biomanipulation of aquatic communities. *Arch. Hydrobiol.* 130:1–33
  134. Reynolds CS. 1984. *The Ecology of Freshwater Phytoplankton*. Cambridge, UK: Cambridge Univ. Press
  135. Riemann B, Sondergaard M, Schierup HH, Bossel-Mann S, Christensen G, et al. 1982. Carbon metabolism during a spring diatom bloom in the eutrophic Lake Mosso, Denmark. *Int. Rev. Gesamten Hydrobiol.* 67:145–85
  136. Rosenzweig ML. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–87
  137. Rosenzweig ML. 1995. *Species Diversity in Space and Time*. Cambridge, UK: Cambridge Univ. Press
  138. Sanni S, Waervagen SB. 1990. Oligotrophication as a result of planktivorous fish removal with rotenone in the small, eutrophic, Lake Mosvatn, Norway. *Hydrobiologia* 200/201:263–74
  139. Sarnelle O. 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* 73:551–60
  140. Sarnelle O. 1994. Inferring process from pattern: trophic level abundances and imbedded interactions. *Ecology* 75:1835–41
  141. Sarnelle O. 1996. Predicting the outcome of trophic manipulation in lakes—a comment on Harris (1994). *Freshwater Biol.* 35:339–42
  142. Schindler DW, Armstrong FA, Holmgren SK, Brunkill GJ. 1971. Eutrophication of lake 227, Experimental Lakes Area, Northwest Ontario, by addition of phosphorus and nitrates. *J. Fish. Res. Board Can.* 28:1763–82
  143. Schmitz OJ. 1994. Resource edibility and trophic exploitation in an old-field food web. *Proc. Natl. Acad. Sci. USA* 91:5364–67
  144. Schoenberg SA, Carlson RE. 1984. Direct and indirect effects of zooplankton grazing on phytoplankton in a hypereutrophic lake. *Oikos* 42:291–302
  145. Shapiro J. 1990. Biomanipulation: the next phase—making it stable. *Hydrobiologia* 200/201:15–27
  146. Shapiro J. 1990. Current beliefs regarding dominance by blue-greens: the case

- for the importance of CO<sub>2</sub> and pH. *Ver. fur theor. angew. Limnol., Verhandlungen* 24:
147. Deleted in proof
  148. Shortreed KS, Stockner JG. 1986. Trophic status of 19 subarctic lakes in the Yukon Territory. *Can. J. Fish. Aquat. Sci.* 43:797–805
  149. Smith FE. 1969. Effects of enrichment in mathematical models. In *Eutrophication: Causes, Consequences, Corrections*. Washington, DC: Natl. Acad. Sci.
  150. Stenson JAE, Bohlin T, Henrikson L, Nilsson BI, Nyman HG, et al. 1978. Effects of fish removal from a small lake. *Verh. Int. Verein. Limnol.* 20:794–801
  151. Stenson JAE, Svensson JE. 1994. Manipulations of planktivore fauna and development of crustacean zooplankton after restoration of the acidified Lake Gardsjön. *Arch. Hydrobiol.* 131:1–23
  152. Stockner JG, Shortreed KS. 1989. Algal picoplankton production and contribution to food-webs in oligotrophic British Columbia lakes, Canada. *Hydrobiologia* 173:151–66
  153. Strong DR. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747–54
  154. Tátrai IL, Tóth G, Istánovics V, Zlinsky J. 1990. The importance of higher trophic level in the process of eutrophication in enclosure. *Int. Rev. ges. Hydrobiol.* 75:175–88
  155. Taylor WD, Hiatt FA, Hern SC, Hilgert JW, Lambou VW, et al. 1978. *Distribution of phytoplankton in Florida lakes*. EPA-600/3-78-085. Las Vegas: USEPA
  156. Tilman D. 1982. *Resource Competition and Community Structure*. Princeton, NJ: Princeton Univ. Press
  157. Tilman D, Pacala S. 1993. The maintenance of species richness in plant communities. In *Species Diversity in Ecological Communities* ed. RE Ricklefs, D Schluter, pp. 13–25. Chicago: Univ. Chicago Press
  158. Turner AM, Mittelbach GG. 1992. Effects of grazer community composition and fish on algal dynamics. *Can. J. Fish. Aquat. Sci.* 49:1908–15
  159. Vadstein O, Harkjen BO, Jensen A, Olsen Y, Reinertsen H. 1989. Cycling of organic carbon in the photic zone of a eutrophic lake with special reference to the heterotrophic bacteria. *Limnol. Oceanogr.* 34:840–55
  160. Vance RR. 1978. Predation and resource partitioning in one-predator-two prey model communities. *Am. Nat.* 112:797–813
  161. van der Molen DT, Boers PCM. 1996. Changes in phosphorus and nitrogen cycling following food web manipulations in a shallow Dutch lake. *Fresh. Biol.* 35:189–202
  162. van Donk E, Grimm MP, Gulati RD, Klein Breteler JPG. 1990. Whole-lake food-web manipulation as a means to study community interactions in a small ecosystem. *Hydrobiologia* 200/201:275–89
  163. Vanni M.J. 1987. Effects of nutrients and zooplankton size on the structure of a phytoplankton community. *Ecology* 68:624–35
  164. Vanni MJ. 1996. Nutrient transport and recycling by consumers in lake food webs: implications for algal communities. In *Food Webs: Integration of Patterns and Dynamics*, ed. GA Polis, KO Winemiller, pp. 81–95. New York: Chapman & Hall
  165. Vanni MJ, Findlay DL. 1990. Trophic cascades and phytoplankton community structure. *Ecology* 71:921–37
  166. Vanni MJ, Layne CD. 1996. “Top-down” trophic interactions in lakes: effects of fish on nutrient dynamics. *Ecology* 78:1–20
  167. Vanni MJ, Layne CD, Arnott SE. 1996. Nutrient recycling and herbivory as mechanisms in the “top-down” effect of fish on algae in lakes. *Ecology* 78:21–40
  168. Vanni MJ, Luecke C, Kitchell JF, Allen Y, Temte J, et al. 1990. Effects on lower trophic levels of massive fish mortality. *Nature* 344:333–35
  169. Van Valen L. 1973. Pattern and the balance of nature. *Evol. Theor.* 1:31–49
  170. Wagner KJ. 1986. *Biological management of a pond ecosystem to meet water use objectives. Lake and Reservoir Management EPA 1986 EP8.2:1 141985*
  171. Watson S, McCauley E. 1988. Comparing patterns of net- and nanoplankton production and biomass among lakes. *Can. J. Fish. Aquat. Sci.* 45:915–20
  172. Watson S, McCauley E, Downing JA. 1992. Sigmoid relationships between phosphorus, algal biomass, and algal community structure. *Can. J. Fish. Aquat. Sci.* 49:2605–10
  173. Wetzel RG. 1983. *Limnology*. Philadelphia: Saunders. 2nd ed.
  174. White TCR. 1978. The importance of relative shortage of food in animal ecology. *Oecologia* 33:71–86
  175. White TCR. 1993. *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Berlin: Springer-Verlag
  176. Wollkind DJ. 1976. Exploitation in three trophic levels: an extension allowing

- intraspecific carnivore interaction. *Am. Nat.* 110:431–47
177. Wootton JT. 1995. Effects of birds on sea urchins and algae: A lower-intertidal trophic cascade. *Ecoscience* 2:321–28
178. Yan ND. 1986. Empirical prediction of crustacean zooplankton biomass in nutrient-poor Canadian Shield lakes. *Can. J. Fish. Aquat. Sci.* 43:788–96
179. Yan ND, Lafrance CJ, Hitchin GG. 1982. Plankton fluctuations in a fertilized, acidic lake: the role of invertebrate predators. In *Acid Rain and Fisheries*, ed. TA Haines, RE Johnson. Bethesda, MD: Am. Fisheries Soc.