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Trophic cascade and biomanipulation: Interface of research and management—A reply to the comment by DeMelo et al.

DeMelo et al. (1992) present a provocative review of food-web experiments. Their open challenge to the conclusions of several studies is sure to evoke controversy. Food-web research in lakes has advanced to the point where a rigorous re-examination of accumulated results is beneficial, and we applaud this effort.

The purpose of our comment is to question some of the conceptual and philosophical claims of DeMelo et al. We do not intend to argue about the case studies they reviewed. Rather, we wish to make three main points: the trophic cascade is not a single-factor theory; the results presented by DeMelo et al. do not contradict the trophic cascade hypothesis; and biomanipulation experiments can provide necessary and critical tests of the trophic cascade hypothesis.

DeMelo et al. regard "biomanipulation," "trophic cascade," and "top-down" ideas as a single unified theory. However, the issues addressed in a trophic cascade hypothesis (Carpenter 1988a) are not directly equivalent to the goals of biomanipulation (Gulati et al. 1990) for the same reason that research is not management. We will elaborate this point later. First, we reiterate our view of the trophic cascade.

Our introductory paper described a trophic cascade hypothesis designed to explain the 50% or so of observed variability in primary production that could not be attributed to nutrient loading (Carpenter et al. 1985). That paper, derived from a grant proposal written in 1982, came at a time when

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Eutrophication study in freshwater has turned into a phosphorus bandwagon. Oblivious to the large amount of variance about the phosphorus inputs—chlorophyll relationship, whatever its form, investigators are repeating studies of this same general model—it's the "in" thing to do. . . . My guess is that the existing model cannot be further refined without incorporation of other factors—for example, the effects of grazing or regeneration of nutrients from sediments by organisms. [Schindler 1981, p. 78]

The trophic cascade idea traces its limnological roots to the observations of Hrbáček et al. (1961) and the hypothesis of Brooks and Dodson (1965); it owes its name to R. T. Paine (1980). As currently expressed, it proposes that predator-prey interactions are transmitted through food webs to cause variance in phytoplankton biomass and production at constant nutrient load (Carpenter et al. 1985) and that the responses are nonlinearly related to the strength of interactions among adjacent trophic levels (Crowder et al. 1988, figure 10.4). It is important to note that "cascading trophic interactions and nutrient loading models are complementary, not contradictory" (Carpenter et al. 1985, p. 634). If variance explained by trophic interactions adds to variance explained by nutrient load, then we can build on the foundation of nutrient research already laid by limnologists. Contrary to the claims of DeMelo et al., the trophic cascade argument attempts to place food-web interactions in the context of the multiple physicochemical factors that govern lake dynamics. Our models are explicit about multifactorial regulation of productivity (Carpenter and Kitchell 1987; Carpenter 1988b) and recognize the multiple causality problem so common in ecological systems (Hilborn and Stearns 1982). Clearly, we agree with DeMelo et al. in their opposition to monistic thinking.

The emphasis on variance distinguishes the trophic cascade hypothesis from otherwise similar ideas of Hairston et al. (1960),

Brocksen et al. (1970), Oksanen et al. (1981), and Persson et al. (1988). The temporal variability of lakes is the proving ground of the cascade hypothesis. In designing tests for these ideas, we have favored an experimental approach (Carpenter 1988a; Carpenter and Kitchell 1988; Carpenter et al. 1991). Paleolimnological reconstructions (Kitchell and Carpenter 1987; Leavitt et al. 1989; Carpenter and Leavitt 1991), long-term records (Mills et al. 1987; Jassby et al. 1990), and multilake comparative studies (Mills and Schiavone 1982; Pace 1984; Carpenter et al. 1991) have also provided valuable evidence. Since DeMelo et al. restrict their scope to experiments, we will not address other research approaches in our comment.

We have argued that whole-lake experiments with substantial, sustained manipulations provide the most crucial tests of the trophic cascade hypothesis (Kitchell et al. 1988; Carpenter and Kitchell 1988; Carpenter 1989). Cascading effects evident in small enclosures (DeMelo et al., figure 1) are interesting but not directly germane. Enclosure results, whether positive or negative, can be irrelevant at the scale of lakes. Many examples demonstrate effects of container size on the results of nutrient limitation and (or) predation studies (Gerhart and Likens 1975; Schindler 1987; Stephenson et al. 1984; Bloesch et al. 1988; Carpenter and Kitchell 1988). Whole-lake results are not subject to these constraints and, therefore, provide a stronger test of the theory. This point is often misunderstood to be a general condemnation of enclosure experiments. It is not. Enclosure experiments can be a valuable tool when properly scaled for the study of particular mechanisms, interactions, or flux rates (Frost et al. 1988) but can be misleading when results are extrapolated to the scale of entire systems.

Strong manipulations (i.e. manipulations that cause substantial and sustained shifts in higher trophic levels) provide more critical tests than weak manipulations (Hurlbert 1984; Kitchell et al. 1988; Carpenter and Kitchell 1988; Carpenter 1989). Results derived from weak treatments can be equivocal because the manipulation was insufficient or because the effect was not apparent.

Too often, those cannot be distinguished. Because manipulation strength depends on the temporal variability of the system as well as the magnitude of change in planktivory (Carpenter 1989), and the latter could be defined many ways, the data of DeMelo et al. (figure 1) on manipulation strength are difficult to evaluate. In any case, the fact that only one strong manipulation of food-web structure was performed in a lake or pond shows that we need much more large-scale experimentation before the role of manipulation strength can be evaluated empirically.

Certain conclusions of DeMelo et al. depend on accepting the null hypothesis that treatment of higher trophic levels had no effect on lower ones. Many of the negative experimental outcomes reviewed by DeMelo et al. stemmed from failure to reject the null hypothesis. However, failure to reject a null hypothesis is not sufficient evidence for accepting it (Peterman 1990a,b). Acceptance of the null hypothesis would require a more elaborate power analysis that considered error variance, number of replicates, and critical *P*-value used in the test (Peterman 1990a,b). The power curve would also depend on the alternative hypotheses, which could be expressed as a continuum of treatment strengths (Carpenter 1989). The negative results found by DeMelo et al. may derive from insufficient treatment strength, lack of replication, overwhelmingly large error variance, overly stringent criteria for evaluating type 1 error, or a null hypothesis that is in fact true (Peterman 1990a,b). We do not have the evidence to decide among these alternatives. From the evidence presented in their table 5, there is no basis for the conclusion of DeMelo et al. that upper trophic levels have no effect on lower ones.

An alternative interpretation of the DeMelo et al. review is that food-web effects are real and common but not universally demonstrated in the conservative variables that express ecosystem responses (e.g. primary production rates, phytoplankton biomass, chlorophyll concentration, or Secchi depth). Schindler (1987) provided strong evidence of the compensatory capacity of perturbed limnetic systems and argued that the response variables offering greatest eco-

logical insight are those of populations and community composition. That follows from the many and diverse examples that most consumers are selective and that aquatic communities are heavily influenced as a result (Kerfoot and Sih 1987). The compensatory response capacity of aquatic communities remains a fertile ground for future work (DeAngelis et al. 1989), offers immense potential for basic research, and has direct relevance to management in that the proximate problems of water quality often revolve around finding ways to reduce or eliminate noxious species (Cooke et al. 1986; Gulati et al. 1990).

Another interpretation is that response to experimental treatment is highly dependent on time. Plankton assemblages have short generation times and rapid response capacity. Although compensatory responses by existing populations can be almost immediate, they will be incomplete in the system sense because the history of previous interactions has excluded some to many species that may soon become major components of the community. The complex of species interactions induced by the "disturbance" of a major change in piscivore or planktivore populations is more likely to exhibit lags that scale to the life histories of the top consumers and to the colonizing capabilities of rare or new members of the community. Evidence of those effects will typically take more time than the duration of most experiments. Recent results of paleolimnological studies offer confirmation of lag effects and the encouragement of an approach that can serve as a surrogate for long-term studies (Leavitt et al. 1989; Carpenter and Leavitt 1991).

In sum, the results of DeMelo et al. are far from being a "disconfirmatory synthesis." Their survey does show that many tests of trophic cascade hypotheses are not conclusive because experiments were equivocal statistically, performed at inappropriate scales, or involved weak manipulations. We endorse their call for rigorous criteria. More tests, and more critical tests, are needed. Further, the static views of traditional statistics seem too often insufficient to the evaluation of dynamic systems (Matson and

Carpenter 1990). For the reasons given above, we argue that substantial, sustained manipulations at the whole-lake scale provide the most critical tests. Because we should expect and test for variability, manipulations arrayed across the variety of lake types will be most valuable. Given the current and expected constraints on research budgets, we should welcome the important potential source of evidence that may derive from biomanipulation experiments performed in collaboration with management agencies.

When coined by Shapiro et al. (1975), biomanipulation referred to a set of management techniques that depended for their success on biological control of certain aspects of eutrophication. More recently, usage has narrowed to mean manipulation of the food web to suppress nuisance algae (Shapiro and Wright 1984; Shapiro 1990). Biomanipulation and the trophic cascade hypothesis are obviously connected (Carpenter et al. 1985) but they are not the same. The latter poses testable questions about the causes of variability, while the former seeks to control the result. Experiments that fail to accomplish a change in the target variable may be a disappointment to the water quality manager, but should offer insight to the aquatic ecologist and a lesson to both. Conceptually constrained and weak treatment experiments offer little more than confusion.

Following the advice and experience of resource managers (Walters 1986), we can probably learn best about biomanipulation by doing it. That is because biomanipulation experiments are typically developed for individual lakes that exhibit eutrophication problems and require the immediate attention of water quality managers. The constraint of replication can be mitigated through alternative statistical techniques (Matson and Carpenter 1990). The same factors that demand a lakewide scale in trophic cascade experiments pertain to biomanipulation (Carpenter and Kitchell 1988; Kitchell 1992). Spatial heterogeneity, littoral-pelagic exchange, vertical migrations, and refuges are now seen as critical topics in biomanipulation research (Shapiro 1990;

Lammens et al. 1990). Although lab or enclosure experiments will remain important for tests of key mechanisms (Frost et al. 1988), it is difficult to see how the most crucial questions about biomanipulation can be resolved without whole-lake trials (Shapiro 1990; Lammens et al. 1990; McQueen 1990).

Biomanipulation by enhancement of piscivorous fish stocks offers managers three potential benefits (Kitchell 1992). Recreational fishery improvements are likely, water quality improvements are possible, and public attention to environmental issues is heightened. Where nutrient loading can be reduced, there is a direct and parsimonious means of controlling nuisance algae. We fully agree with DeMelo et al. in this regard. In many cases, however, diffuse nutrient inputs occur and are difficult to control, or efficient internal recycling makes it impossible to diminish nutrient availability through reduction of point sources (Cooke et al. 1986). There is considerable need for innovative approaches to remediate eutrophied lakes that are not susceptible to direct controls of nutrient loading. Experimentation is an essential step in evaluating potential methods like biomanipulation. A biomanipulation experiment is, therefore, an investment in both fishery improvement and new knowledge about a potential method for reducing the frequency and magnitude of noxious algal blooms (Kitchell 1992).

Much of the scientific debate about the mechanisms of trophic interaction is of little relevance to management. From a practical standpoint, it does not matter whether chlorophyll declines via grazing or via sequestration of P in piscivore biomass. Evaluation of biomanipulation hinges on the water quality responses observed at the scale of management: massive piscivore manipulations, in real lakes, over periods of years. The dark shroud of Popperian logic has limited value to managers.

Research and management have different methods, goals, and reward systems. Consequently, they often have incompatible expectations (Cullen 1990). The conservativeness that serves science well can lead to inaction in management. A recent example

highly relevant to limnologists is the controversy over acid precipitation effects. Should emission controls be enacted early, while considerable uncertainty remains? Or should we wait until 95% of the experts agree that all of the scientific evidence is unequivocally confirmed at rigorous levels of statistical precision? Neither course is "unscientific." Emission controls are in fact a large-scale experiment from which enormous scientific insights could develop if appropriate before-and-after studies were designed (Walters 1986, p. 338-343). In this case, our society is unlikely to suffer the luxury of a pure scientific truth.

It would be interesting to expose the nutrient paradigm to similar scrutiny (Persson et al. 1988). Its early development was fraught with controversy, inconclusive experiments, and conflicting evidence. Lakes were dredged, drained, lined with plastic, aerated, alumped, and filtered. Promise proved insufficient in many cases but some techniques were successful in some places and remain among the tools used by lake managers (Cooke et al. 1986). Perhaps the most important insights emerged from strong treatment effects at the whole-lake scale (Schindler 1987). Issues surrounding macrophyte harvesting and alkalization of lakes regularly appear in the current literature as evidence that a similar winnowing and sifting occurs when research efforts and public concerns converge on an important problem.

Biomanipulation and the trophic cascade hypothesis are at a remarkable confluence of research interests and management applications. Both demand large-scale field trials best regarded as experiments (Kitchell 1992). Because theory predicts variable results, multiple field trials are needed in lakes that differ in catchment geochemistry, littoral zone development, trophic state, and food-web composition (Carpenter 1989; McQueen 1990; Gulati et al. 1990). We do not offer this recommendation as a "... more work is necessary" excuse. Our assertion is based on the reality that lakes differ and that those idiosyncracies must be accounted for in a more general theory regarding the causes and controls of variabil-

ity. We may learn that we can neither understand nor control variability; that we must "... embrace uncertainty" (Walters 1986). That conclusion is fully acceptable but should not be based on weak evidence.

The disagreement and controversy described by DeMelo et al. are symptoms of intellectual ferment driven by the best creative effort of aquatic ecologists and are among the reasons that limnology is not withering (Jumars 1990). Researchers and managers engaged in biomanipulation participate in a process of learning by doing, which necessarily involves collective debate of a varied array of case studies. At another level, this process can be regarded as a branch in the difficult evolution of productive relationships between basic ecology and resource management (Lubchenco et al. 1991). The boundary between research and management is indeed turbulent (Cullen 1990). In the case of the trophic cascade hypothesis and biomanipulation, we feel that boundary turbulence indicates high coefficients for diffusion of mutual understanding. Progress is a process rarely punctuated with final solutions.

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