ASLO Limnology and Oceanography

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Author(s): Rita DeMelo, Robert France, Donald J. McQueen
Source: *Limnology and Oceanography*, Vol. 37, No. 1 (Jan., 1992), pp. 192-207
Published by: American Society of Limnology and Oceanography
Stable URL: http://www.jstor.org/stable/2837773
Accessed: 23/09/2009 10:52

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COMMENT

Limnol. Oceanogr., 37(1), 1992, 192–207
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Biomanipulation: Hit or myth?[1]

> The suggestion . . . that changes in fish community structure could alter the biomass and community structure of zooplankton and phytoplankton is now clearly confirmed—Carpenter (1988, p. 120).

> Given the strong propensity among ecologists to promote "bandwagons" or particular approaches to particular problems . . . we urge caution in moving too rapidly toward management with food-web manipulations—Crowder et al. (1988, p. 155).

Lake biomanipulation theory (Shapiro and Wright 1984) is based on the prediction that increased piscivore abundance will result in decreased planktivore abundance, increased zooplankton abundance, and increased zooplankton grazing pressure leading to reductions in phytoplankton abundance and improved water clarity. Biomanipulation is now at a stage of becoming ensconced as a lake management tool and accepted irrefutably in the generalist literature (e.g. Carpenter et al. 1985; Carpenter and Kitchell 1988; Townsend 1988; Int. Jt. Comm. 1988), the literature dealing with nonaquatic communities (Spiller and Schoener 1990) and the press (Stevens 1990). Once enthroned, a theory becomes envisioned as unassailable and definitive dogma (Wittgenstein *cited by* Popper 1968) and its speculations can be elevated to the status of ecological laws merely by the passage of time (McIntosh 1980; Loehle 1987). This deification is unhealthy, because even the briefest perusal of the pertinent literature indicates that, far from being "robust" (sensu Levins 1966), the biomanipulation/trophic-cascade/top-down theory may be unsoundly based on many half-truths and much hand-waving (sensu Stenseth 1983) and overextrapolation of the data.

Recent enclosure and whole-lake experiments have questioned the validity of biomanipulation as an effective management technique for the control of phytoplankton abundance (e.g. Post and McQueen 1987; Threlkeld 1988; McQueen et al. 1989), and others have pointed out that apparent biomanipulation successes may not have been caused by the cascading effects of zooplankton feeding on phytoplankton, but resulted from several of alternate food-web interactions (Vanni and Findlay 1990). Are these examples merely atypical anomalies (sensu Kuhn 1962) or rather do they reflect a systematic disharmony or incompetence (Feyerabend 1988) in the biomanipulation theory to adequately address the majority of natural phenomena?

Because corroboration is paramount to the success of any theory (Loehle 1987), it is important to critically examine the scientific evidence used to support the biomanipulation case; i.e. to determine whether the statements espoused by the theory can be justified by perceptual experience (Popper 1968).

Diamond (1986) recently developed a 10-point strategy, paralleling that used by epidemiologists, for testing putative and com-

[1] Submitted: 21 September 1990.

Acknowledgments

This work was funded by a Natural Sciences and Engineering Research Council (Canada) grant to D.J.McQ. and by an NSERC PDF fellowship to R.F. We thank Steven Threlkeld, Ray Drenner, Steven Carpenter, and Don Hall for their comments.

peting explanations. Those points germane to an examination of biomanipulation theory include the following questions. Is the proposed association consistent over many experimental sites or with different populations? Does the size of the experimental effect reflect the degree of perturbation? Is this association manifest over a wide range of variation in other variables? Can the observed effect be predicted quantitatively from the putative causal mechanism?

The purpose of our study is to critically review results from the biomanipulation/trophic-cascade literature to assess the consistency (first point above) and the dose-response gradient (second point above) of the results. We also review the results in relation to gradients of scale (third point above) in terms of size of the experimental system, duration of the experiment, extent of fish manipulation, and system productivity. Finally we attempt to assess quantitative predictions (fourth point) with respect to causal mechanisms. We hope that our study will demythologize the theory of biomanipulation and constructively challenge the managerial aspirations of those currently championing its use.

Our approach was to examine 50 papers documenting 44 independent food-web biomanipulations published between 1961 to 1989 and to assess agreement with the between-trophic level patterns predicted by the biomanipulation/trophic-cascade/top-down hypothesis. Of these 44 studies, 18 were based on experiments conducted in enclosures either in the laboratory or in situ placements in the field and 26 involved pond or lake manipulations or comparisons. Studies pertaining to only two levels of trophic interaction (i.e. fish–zooplankton or zooplankton–phytoplankton) were excluded from consideration. Limnological details of the pond and lake study sites are arranged by publication date in Table 1.

Composite working tables (not shown) were constructed summarizing the results for each study. This detailed examination included the following variables: piscivore and vertebrate planktivore densities or biomasses; *Chaoborus* or other invertebrate planktivore densities; total zooplankton biomass or density and body size; cladoceran, daphnid, copepod, bosminid, and (or) rotifer densities or biomasses and body sizes; total phytoplankton, blue-green, green, diatom, and (or) cryptophyte biomass or cell volume or Chl *a* or primary production; Secchi depth or light transmittance; P and N concentrations; and pH. To more clearly analyze patterns of agreement or disagreement with biomanipulation predictions, we condensed the responses of the principal trophic levels from the composite tables into the following metrics: piscivore abundance, vertebrate planktivore abundance, zooplankton abundance, phytoplankton abundance, and Secchi depth. Judgments concerning the integrated response of each trophic level were based on the individual responses of the various parameters from the composite tables. Where divergent responses occurred within each of the integrated trophic strata, weight was placed on the response of the most important individual parameter as suggested from biomanipulation theory (e.g. abundances of cladoceran zooplankton and of cyanobacteria or green algae).

We have summarized our analyses in Tables 2 and 3. For each study, complete agreement with the predictions of the top-down (biomanipulation/trophic-cascade etc.) hypothesis is indicated with "Y" which signifies that causative predator–prey interactions were verified. Complete disagreement is indicated with "N" which signifies that predator–prey interactions were not responsible for the observed result. In cases where agreement is ambiguous, unknown or undecided a "U" is recorded and explanations are provided in Table 4. Occasionally these explanations represent disagreements between our interpretations of the data and the interpretations offered by the investigators. In these cases there may have been statistical problems, insufficient data, ambiguous interpretations, or confounding. More often the investigators have identified these difficulties and most often these involved confounded results.

These results are summarized in Table 5. Together there were data for 118 response cells. Fifty-two represented complete agreement with the predictions of the top-down models. Twenty-one represented complete

Table 1. Description of limnological characteristics of lake or pond environments. Studies are listed in general chronological order.

Study	Name and location of lake or pond	Trophic status*	Total P (μg liter^{-1})	Surface area (ha)	Mean depth (m)	Max depth (m)	Native fish species	Stocking rate	P loading
Hrbáček et al. 1961	Poltruba, Czechoslovakia	—	150	0.18	2.77	5.56	Various	—	—
Grygierek et al. 1966	Manmade ponds, Poland	—	—	0.2	1	—	—	—	—
Hall et al. 1970	Ponds, Cornell Univ., N.Y.	—	17 (1966)–64 (1965)	0.07	—	1.3	—	—	—
Losos and Hetesa 1973	Ponds, state fishery, Poland	—	—	0.05	0.12	0.15	—	—	50 kg ha^{-1}
Hrbáček et al. 1978; Hrbáček et al. 1986	Hubenov and Vrchlice Reservoirs, Czechoslovakia	E	30 mg m^{-3}	0.516; 0.925	8.93	31.5	Brown trout, rainbow trout; roach, perch, cyprinids	—	—
Spodniewska and Hillbricht-Ilkowska 1978; Hillbricht-Ilkowska and Weglenska 1978	Lake Warniak, Poland	E	—	38.4	1.5	3.7	Carp, bream	893 kg carp, 849 kg bream	—
Stenson et al. 1978; Henrikson et al. 1980	Lilla, Stockelidsvatten, Behuslan, Sweden	O	—	1	—	8	Roach	—	—
Fott et al. 1980	Velký Pálenec, Czechoslovakia	E	—	31	1.4	—	Carp, whitefish	—	—
Leah et al. 1980	River Yare, Brundall, U.K.	H	2,000 (summer)	—	1.2	—	—	—	—
Lynch 1979; Lynch and Shapiro 1981	Pleasant Pond, Minn.	—	—	0.25	2.5	—	Fathead minnows	—	—
Benndorf et al. 1984	Flooded quarry, Germany	M	—	0.044	7	—	Various	—	—
Gophen 1984, 1985*a,b*	Lake Kinneret, Israel	E	12	25,200	24	42	Various	—	—
Olrik et al. 1984	Lake Hjarbaek Fjord, Denmark	H	300	2.4	2	—	Various	107 t yr^{-1} TP	—
Reinertsen and Olsen 1984	Haugatjern, Norway	E	15	9.1	7.6	15.5	Whitefish, perch	—	—
Shapiro and Wright 1984	Round Lake, Minn.	E	47.8	12.6	2.9	10.5	Various	—	—

Table 1. Continued.

Study	Name and location of lake or pond	Trophic status*	Total P (μg liter^{-1})	Surface area (ha)	Mean depth (m)	Max depth (m)	Native fish species	Stocking rate	P loading
Spencer and King 1984	Ponds, Mich.	H	100	3.3–5.0	—	1.8	—	—	0.1 mg liter^{-1}
Vijverberg and Van Densen 1984; Lammens 1988	Tjeukemeer, Netherlands	E	—	2,150	1.5	—	Various	—	—
Komarkova et al. 1986	Spolsky Pond, Czechoslovakia	E	108	124.3	2.09	4.8	—	Carp, 328–467 kg ha^{-1}	—
Komarkova et al. 1986	Ruda Pond, Czechoslovakia	E	130	72.5	1.3	2.4	—	Carp, 226–768 kg ha^{-1}	—
Scavia et al. 1986; Lehman 1988	Lake Michigan	O	5–8	5.8×10^6	84	285	Various	$7.4–16 \times 10^6$ salmonids	—
Wagner 1986	Johnson Bass Pond, N.J.	E	23.7	1.4	2.7	5	Various	—	—
Carpenter et al. 1987	Tuesday Lake, Mich.	O	0.79	10	18.5	—	—	Plus 466 largemouth bass, minus 90% minnows	—
Carpenter et al. 1987	Peter Lake, Mich.	O	2.4	8.3	19.3	—	—	Minus 90% bass, plus 44,901 minnows	—
Mills et al. 1987	Oneida Lake, N.Y.	E	30–99	20,700	6.8	—	Various	—	0.72 g m^{-1} yr^{-1}
Ranta et al. 1987	Rock pools, Finland	E	—	$2–8 \times 10^{-4}$	—	0.25, 0.45	—	—	—
Benndorf et al. 1988	Bautzen Reservoir, Germany	H	—	533	7.4	—	Roach, perch, pikeperch	—	4.1–15.5 g m^{-1} yr^{-1}
McQueen et al. 1989	Lake St. George, Ont.	M	17–27	10.6	—	15.2–16.2	Various	—	17–27 μg liter^{-1}

* E—eutrophic; H—hypereutrophic; M—mesoeutrophic; O—oligotrophic.

Table 2. Lake and pond studies. Details of the manipulation and trophic level responses. Fish—piscivore density or biomass; plankt.—planktivore density or biomass: I—increased fish, D—decreased fish. Zoo.—total or large zooplankton density or biomass; phyto.—biomass or chlorophyll *a*. Y—agrees with the predictions of top-down theories; N—no agreement; U—unknown or undecided about agreement with predictions of the top-down hypothesis (in all cases details are listed in Table 4). (No data available: —.)

	Manipulation					Observed responses between trophic levels				
Study	Method	Duration	Fish species	Stocking rate	Nutrient loading	Fish	Plankt.	Zoo.	Phyto.	Secchi depth
Hrbáček et al. 1961	Rotenone	Apr–Oct 57	—	—	—	I	D	Y	Y	Y
Grygierek et al. 1966	Stocking	1957–1961	Carp fry	12.5–150 kg ha^{-1}	—	—	I	N	U	—
Hall et al. 1970	Stocking and nutrient enrichment	Jun–Oct 67	Bluegill sunfish	47 kg ha^{-1}	0–272 kg $week^{-1}$ fertilizer	—	I	Y	N	—
Losos and Hetesa 1973	Stocking and nutrient enrichment	Jul–Aug 63, 64	Carp fry	38.4 kg ha^{-1} (1963), 9.6 kg ha^{-1} (1964)	300–600 kg ha^{-1} fertilizer	—	I	Y	Y	Y
Hrbáček et al. 1978; Hrbáček et al. 1986	Sampling	Apr–Dec 76; 1978–1983	—	—	—	—	I	U	U	U
Spodniewska and Hillbricht-Ilkowska 1978; Hillbricht-Ilkowska and Weglenska 1978	Sampling	Apr–Oct 67–69	—	—	—	—	I	Y	N	—
Stenson et al. 1978; Henrikson et al. 1980	Rotenone	1973–1976	—	—	—	—	D	Y	U	U
Fott et al. 1980	Sampling	May, Aug–Sep 75–79	—	Up to 1,880 kg ha^{-1} carp and 60 kg ha^{-1} whitefish	—	—	I	Y	U	U
Leah et al. 1980	Sampling	1976–1977	—	—	—	I	Y	Y	U	U
Edmondson and Litt 1982	Sampling	1971–1980	—	—	—	—	Low	N*	N*	N*
Lynch 1979; Lynch and Shapiro 1981	Sampling	Apr–Aug 76	Fathead minnows	—	—	—	I	Y	U	—

Table 2. Continued.

Study	Manipulation					Observed responses between trophic levels				
	Method	Duration	Fish species	Stocking rate	Nutrient loading	Fish	Plankt.	Zoo.	Phyto.	Secchi depth
Gophen 1984, 1985*a,b*	Sampling	1969–1981	—	—	—	—	High	Y	U	—
Olrik et al. 1984	Sampling	Mar–Oct 81	—	—	—	—	Low	Y	U	—
Reinertsen and Olsen 1984	Rotenone	1979–1982	—	—	—	—	D	—	Y	—
Shapiro and Wright 1984	Rotenone and restocking	1980–1982	Bass, walleye, bluegill	1 piscivore : 2.2 plankt.	—	I	—	Y	U	Y
Spencer and King 1984	Sampling	Jun–Nov 79	Fathead minnows, brook sticklebacks	—	—	—	I	Y	U	U
Vijverberg and Van Densen 1984; Lammens 1988	Sampling	1976–1982	—	—	—	I	Y	Y	N	—
Komarkova et al. 1986	Sampling	Apr–Aug 76–78	—	21–694 kg ha^{-1}	—	—	I, D	U	U	U
Scavia et al. 1986; Lehman 1988	Sampling	1975–1984	—	—	—	I	Y	Y	N	U
Wagner 1986	Piscivore stocking and plankt. removal	1984–1985	Various	+70 piscivores, −700 plankt.	—	I	D	U	U	U
Carpenter et al. 1987	Piscivore stocking and plankt. removal	Jun–Sep 80	Largemouth bass, minnows	+466 bass, −90% minnows	—	I	D	Y	Y	—
Carpenter et al. 1987	Piscivore removal and plankt. stocking	Jun–Sep 80	Largemouth bass, minnows	−90% bass, +44,901 minnows	—	D	I	N	N	—
Mills et al. 1987	Sampling	1969–1977	—	—	—	I	Y	Y	U	U
Ranta et al. 1987	Two pools, separation and stocking	78 d 91 d	Tench	3, 5, and 7 fish	—	—	I	U	Y	—
Benndorf et al. 1984, 1988	Catch restriction and stocking	1977–1985	Perch, pikeperch	20,000–80,000 pikeperch yr^{-1}	—	High	Y	Y	N*	Y
McQueen et al. 1989	Sampling	1980–1986	—	—	—	I	Y	U	N	N

* Details in Table 4.

Table 3. Enclosure studies. Details of manipulation, data interpretations, and assessments of agreement or disagreement with the top-down hypothesis. Abbreviations same as Table 2.

	Manipulation						Observed responses between trophic levels				
Study	Surface area (ha)	Duration	Fish species	Stocking rate	Nutrient loading	Total P (μg liter^{-1})	Fish	Plank.	Zoo.	Phyto.	Secchi depth
Hurlbert et al. 1972	0.0012	1970–1971	*Gambusia affinis*	50 fish pond^{-1}	—	30–400	—	I	Y	U	U
Andersson et al. 1978	0.0007	Jun–Oct 76	Bream, roach, crucian carp	90 and 220 g m^{-2}	—	359	—	I	U	U	U
Lynch 1979; Lynch and Shapiro 1981	0.78×10^{-4}	40 d, 1975	Bluegill sunfish	100–1,064 kg ha^{-1}	—	109	—	I	Y	Y	—
Hurlbert and Mulla 1981	0.0024	Aug 67–May 68	*G. affinis*	50–450 fish pond^{-1}	—	—	—	I	Y	Y	—
Goad 1984	0.0003	15 d, 1981	Perch, trout	5–50 and 20 g m^{-2}	—	—	—	I	U	U	—
Levitan et al. 1985	0.0003	1979–1980	Creek chubs, trout	6 chubs, 8 trout	1.6–16 μM P, 25–250 μM N	29	—	I	Y	Y	—
Drenner et al. 1986	0.0004	Nov 82, Mar, Jun, Sep 83 (45–53 d)	*Dorosoma, Menidia*	0–271.2 and 0–19.1 g	—	7.8 (SRP)	—	I	Y	N	N
Hambright et al. 1986	0.006	5 Jun–30 Sep 85	Bluegill, largemouth bass	280 and 112 kg ha^{-1}	—	46	I	Y	Y	U	—
McQueen and Post 1986	0.005	Summer 1983–1985	Various	1,363 kg ha^{-1}	—	50	—	D	U	Y	—
McQueen and Post 1986	0.02	May–Sep 82	0+ yellow perch	0, 200, 600 fish	5 g 90% H_3PO_4, 125 g $NaNO_3$	50	—	I	U	U	—
Reinertsen et al. 1986	0.00018	Aug 79–Jun 80	0+ perch, whitefish	800 kg ha^{-1}	—	15	—	I	Y	U	—
Koksvik and Langeland 1987; Langeland et al. 1987	0.0019	5 Jun–30 Sep 80	Whitefish	640–700 kg ha^{-1}	—	7.6	—	I	Y	U	N
McQueen and Post 1988	0.005	7 Jun–25 Oct 85	0+ yellow perch	50 enclosure^{-1}	—	—	—	I	Y	N	N
Post and McQueen 1987	0.005	2 Jun–27 Sep 82	0+ yellow perch	2–5 kg ha^{-1}	5 g P; 126 g N	—	—	I	Y	N	Y

Table 3. Continued.

Study	Manipulation: Surface area (ha)	Duration	Fish species	Stocking rate	Nutrient loading	Total P (μg liter^{-1})	Observed responses between trophic levels: Fish	Plank.	Zoo.	Phyto.	Secchi depth
Threlkeld 1987, 1988	0.0004	(1987) May–Nov 84	*Menidia, Tilapia, Dorosoma*	350 g wet wt		—	—	I	Y	N*	N*
		(1988) May–Dec 85; Mar–May 86	*Menidia*	0–256 tank^{-1}	0–32 dead fish tank^{-1}						
Threlkeld and Drenner 1987	0.0004	271 d	*Dorosoma*	0–249.3 g	—	5.754	—	I	U	U	U
Threlkeld and Drenner 1987	0.0004	271 d	*Menidia, Dorosoma*	0–19.3 and 0–272.3 g	—	5.754	—	I	Y	U	U
Vanni 1987*a,b*	0.00019	Jul–Aug 80, 81	Bluegill sunfish	1 (1980)–2 (1981) enclosure^{-1}	0–10 μg liter^{-1} P, 0–300 μg liter^{-1} N	—	—	I	Y	U	—

* Details in Table 4.

disagreement and 45 were undecided. On first examination, these results might seem to bode well for the top-down hypotheses; however, a more detailed analysis casts doubt on this conclusion. Of the piscivore–planktivore interactions 100% were Y responses and 72% of the planktivore–zooplankton interactions showed that changes in planktivore biomass were associated with zooplankton size and (or) numerical responses and were in agreement with top-down predictions. These strong predator effects at the top of the food web have been documented by others (reviewed by McQueen 1990) and are not surprising. At lower trophic levels, the top-down responses weaken. Only 20% of the zooplankton–Chl *a* and 21% of the zooplankton–Secchi depth responses supported the theory, while 27 and 25% did not. The remaining responses were undecided.

The undecided or ambiguous results noted above (Tables 2, 3) and summarized in Table 5 derived from four sources. One of the most important (22 response cells) involved confounding of the experiments by agents unrelated to the modifying variable in question (i.e. fish predation pressure). In such situations it becomes impossible to distinguish from among the observed effects those that are related directly to biomanipulation. Often the confounding factors were identified by the investigators and included algal grazability (Haney 1987), nutrient or climatic fluctuations (Shapiro and Wright 1984; Carpenter et al. 1987); direct fish effects (Ranta et al. 1987; Threlkeld 1988), and direct and indirect effects of macrophytes (reviewed by McQueen 1990).

Occasionally, our reviews detected confounding that was not identified by the investigators and we have indicated these cases in Table 4. In most cases, confounding was important at the zooplankton–phytoplankton link in the food web, and unless future carefully controlled experiments are undertaken to identify these effects, it will be impossible to separate phytoplankton responses that are due to planktivore-mediated alterations in zooplankton grazing from responses to direct and indirect nutrient additions and competition from fish, macro-

Table 4. Explanations for the symbols recorded in Tables 2 and 3. The studies are listed alphabetically and in cases where more than one paper is involved, the study is listed under the name of the first paper shown in Table 2 or 3.

Andersson et al. 1978: Grazing effects on phytoplankton and water clarity were confounded by direct fish effects (i.e. P regeneration in the Trummen enclosure and bioturbation in both fish enclosures).

Benndorf et al. 1988: Showed that phytoplankton biomass was lower in 1981, but that during 1982–1985 biomasses were higher compared to prebiomanipulation years.

Edmonson and Litt 1982: Attributed changes to bottom-up effects.

Fott et al. 1980: Noted that changes in Chl *a* and transparency are confounded by significant between-year changes in fish biomass and by associated changes in bioturbation and nutrient resuspension.

Goad 1984: Noted that Chl *a* concentrations in the fish and fish-free enclosures were all similar ($\sim 50\ \mu g\ liter^{-1}$) at the end of the experiment. Control zooplankton numbers were erratic and the percent *Daphnia* did not change in two of the three fish enclosures.

Gophen 1984, 1985*a,b*; Gophen et al. 1990: Noted that potential effects of zooplankton on phytoplankton were confounded by changes in nutrient loading and N : P ratios.

Grygierek et al. 1966: Reported that increasing fish stocks resulted in increased densities of crustacean zooplankton and no change in phytoplankton. Data suggested that phytoplankton abundance might have been lower in the zero fish pond.

Hambright et al. 1986: Reported that decreased zooplankton was associated with increased total P and that these confounding influences made it impossible to attribute all of the changes in phytoplankton to either top-down or bottom-up causes.

Hrbáček et al. 1978, 1986: Mean annual Chl *a* in Hubenov Reservoir (between 1976 and 1983) was lower than in Vrchlice, but the differences were not significant. Also, higher Chl *a* values in Vrchlice Reservoir were associated with higher P values. Zooplankton biomass was not significantly different for the two reservoirs, but percentage large cladocera was significantly higher.

Hurlbert et al. 1972: Zooplankton effects on algal groups were nonsignificant in 8 of 12 cases. Higher phosphate concentrations in fish treatments confounded zooplankton grazing impacts on phytoplankton.

Koksvik and Langeland 1987; Langeland et al. 1987: Reported that the presence of whitefish in a limnocorral caused a decline in mean *Daphnia* size and that this resulted in a 1-month (approximate) reduction in total *Daphnia* biomass and increased *Daphnia* numbers in the whitefish limnocorral. During spring and late summer *Daphnia* biomass was equal in both limnocorrals. *Staurastrum luetkemuelleri* increased during late July and August when *Daphnia* biomass was similar in both limnocorrals. During midsummer, phytoplankton biomass was about equal in both limnocorrals.

Komarkova et al. 1986: Chl *a* increased with zooplankton biomass. The other mean annual trophic level correlations had the sign predicted by the top-down models, but none were significant.

Leah et al. 1980: In the inner fish-free broad, Chl *a* decreased when filter-feeding crustaceans increased for ~ 1 month in 1977. During the 18 months before and after this clear-water phase there was no relationship between Chl *a* concentration (or water clarity) and crustacean biomass. The results may have been confounded by direct macrophyte effects (shading etc.) on algae.

Lynch and Shapiro 1981; Lynch 1979: Grazer effects on phytoplankton were confounded because the south basin of the pond which contained fathead minnows also had total P levels that were, by the end of summer, three times higher than the north basin which contained walleye.

McQueen and Post 1986: Reported that zooplankton biomass decreased in response to increasing fish biomass, but the enclosure data for 1983 indicated comparable values for zooplankton biomass at medium to low biomasses of fish. The authors reported that Chl *a* increased in concentration in relation to increased fish biomass in enclosures, but the data showed comparable values for phytoplankton biomass in 1983 when fish biomass was at a medium to low level.

McQueen et al. 1989: Reported that low planktivore numbers in 1982 and 1985–1986 and high planktivore numbers in 1983–1984 were associated with high and low daphnid biomasses, respectively. The data suggested that fish predation exerted a weak impact on zooplankton biomass.

Mills et al. 1987: Except for the spring clear-water phase (May–June 1976–1977), Chl *a* concentrations were not strongly related to changes in daphnid abundance. They were related to changes in total phosphorus.

Olrik et al. 1984: Did not discount the hypothesis that the small chlorococcal green algae declined because of rapidly changing physical conditions (i.e. high pH and NH_4).

Ranta et al. 1987: Noted that zooplankton responses depended upon initial densities and species compositions.

Reinertsen et al. 1986: Noted that the zooplankton–phytoplankton interactions were confounded by the combined effects of grazing and nutrient additions by fish. Zooplankton grazing could have accounted for decreases in *R. lacustris,* but other species were affected by nutrient inputs from fish and by P competition with other phytoplankton species.

Scavia et al. 1986: Lehman (1988) reported no clear correlations between Chl *a* concentrations and daphnid abundance. Water clarity changes were not always associated with changes in grazer abundance.

Shapiro and Wright 1984: Mark-recapture fish estimates were not available. Chl *a* increases during both 1981 and 1982 were not associated with changes in zooplankton or *Daphnia* abundance or mean body size. During the last half of 1981 and during 1982, P levels were lower.

Table 4. Continued.

Spencer and King 1984: Noted that blue-green dominance in planktivore-free ponds was likely due to changes in light penetration and buoyancy. Zooplankton grazing effects on phytoplankton were confounded by direct macrophyte (shading etc.) effects.

Stenson et al. 1978; Henrikson et al. 1980: Improvements in water clarity were reported for spring 1975—2 yr after fish removal and 2 months before the increase in large copepods.

Threlkeld 1987, 1988: Noted that the enclosures containing fish had more phytoplankton and lower Secchi depths, but that this could not be directly attributed to zooplankton grazing. Direct fish effects were also important.

Threlkeld and Drenner 1987: Reported that *Menidia* strongly influenced zooplankton, but had little effect on phytoplankton. *Drosoma* had few residual effects on zooplankton and strong effects on phytoplankton which may have been confounded by fish mortality effects.

Vanni 1987*a,b*: Noted that phytoplankton increases observed in enclosures with fish could not be completely attributed to decreased zooplankton grazing. Nutrient effects were also important.

Wagner 1986: Zooplankton, Chl *a*, and Secchi depth all changed in ways consistent with predictions of the top-down hypothesis. However, only mean summer values were given, so statistical treatments are not possible. Also, changes in zooplankton persisted for only one summer while changes in the fish community persisted for two summers.

phytes, and bottom-up physical-chemical factors.

An equally prevalent category of ambiguity (22 response cells) consisted of studies containing statements pertaining to data that were incomplete or not present in the paper itself and were not easily located in other referenced papers. In such cases we are often asked to accept inferences on faith alone, which has certainly contributed to the creation of the mythology surrounding biomanipulation and occasionally contributes to obscurantism (opposition to the spread of knowledge by deliberate vagueness or abstruseness—Popper 1968).

Attempts to nonobjectively force data to concur with preconceived beliefs in biomanipulation theory (six cases) by explaining away conflicting results (termed "confirmation bias"—Loehle 1987) are what Loehle (1988) calls "just-so-stories." Confirmation bias can occur even when disconfirming evidence that glaringly contradicts the hypothesis is clearly presented (Loehle 1987).

Statistical errors and failure to apply appropriate statistical tests occurred in only six response cells.

Interpretations of patterns and processes of aquatic communities can be strongly influenced by the scales used in the investigations (Frost et al. 1988). Indeed, some of the most vociferous disagreements among ecologists arise from differences in their choice of study scale (Wiens et al. 1986). For example, Carpenter (1988, p. 129) noted that neglecting consideration of scale "may cause biomanipulation attempts to fail, and to lead to premature abandonment of a promising management technique." Do consistent patterns exist in the results obtained from investigations of cascading-trophic interactions in relation to gradients of scale?

We ordered the lake, pond, and enclosure studies to investigate the presence of general response patterns. We used four ordering criteria: physical size of the study site; duration of the experiment; extent of fish manipulation; and system productivity. For each trophic-level interaction from each study (each cell in Tables 2 and 3), the interaction strength was determined as follows: two were scored for each unequivocal

Table 5. Summary of trophic-level interactions for the enclosure experiments and the lake and pond experiments. The numbers in each cell represent the numbers of complete agreements with the predictions of the top-down theories (Y), disagreements (N), and equivocal or undecided interactions (U).

	Piscivore and plankt.	Plankt. and zoo.	Zoo. and Chl *a* or phyto.	Zoo. and Secchi depth
Enclosures (No. of studies: 18)				
Y	1	14	4	1
N	0	0	4	4
U	0	4	10	4
Lakes and ponds (No. of studies: 26)				
Y	6	17	5	4
N	0	3	8	2
U	0	5	13	9

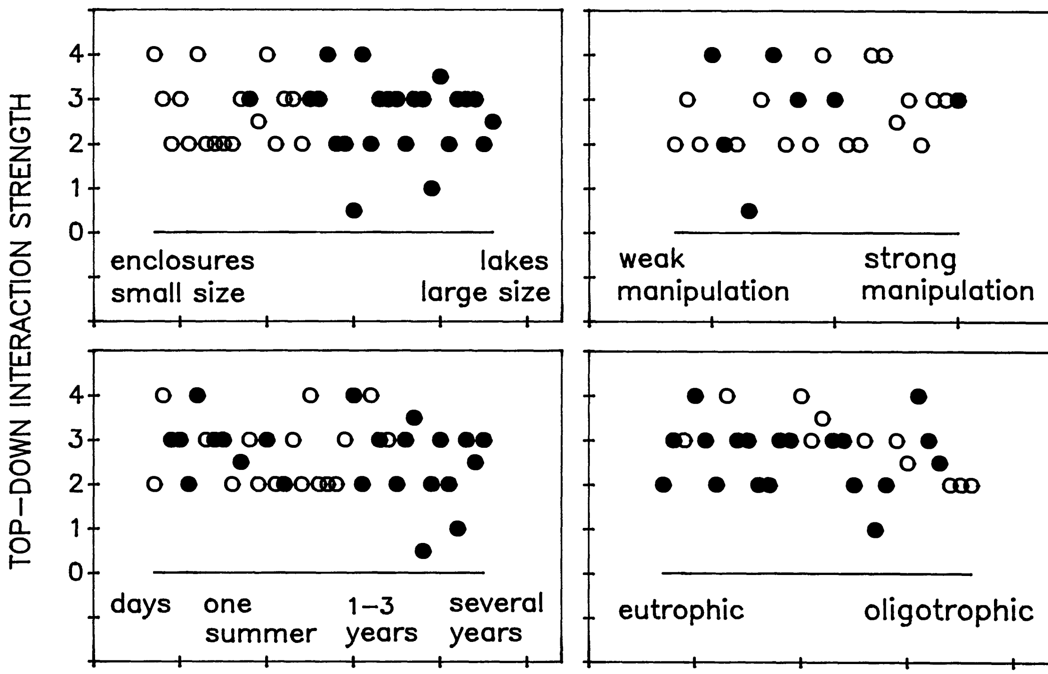

Fig. 1. Interaction strength plotted with respect to four scaling variables. Lower right—interaction strengths are ordered with respect to total P so that the most oligotrophic experiments are plotted on the right and the most eutrophic on the left. Lower left—studies are ordered from those having the shortest duration to those having the longest. Upper right—ordering is in terms of the magnitude of change in planktivore abundance. This ordering is intended to represent changes in magnitude of the top-down biomanipulation. Upper left—studies are ordered from the smallest enclosures to the largest lakes. Total interaction strength is calculated by summing the planktivore–zooplankton interaction strength and the average of the two zooplankton–phytoplankton interaction strengths. Piscivore–planktivore interactions are not included. An interaction strength of four represents perfect agreement of both trophic level interactions with the top-down/biomanipulation predictions. An interaction strength of zero represents complete disagreement. For each analysis, individual studies are represented by a single point (●—pond or lake; ○—enclosure).

agreement with the biomanipulation theory (Y), one was scored for each equivocal or undecided agreement (U), and zero was scored for each disagreement (N) between the data and predictions of the top-down/biomanipulation theory. For each study, the plotted (Fig. 1) interaction strength was calculated by summing the planktivore–zooplankton trophic interaction strength and the average of the two zooplankton–phytoplankton interaction strengths. An interaction strength of four represents perfect agreement at all trophic levels with the top-down biomanipulation predictions. An interaction strength of zero represents complete disagreement.

Kitchell and Carpenter have criticized enclosure studies by suggesting that since they are not conducted at appropriate size scales, they can never determine true causal pathways and are therefore inadequate for assessing patterns in community-wide behavior (Kitchell et al. 1988; Carpenter 1988; Elser and Carpenter 1988; *see also* Sih 1988). Alternatively, although large-scale field experiments remove problems with spatial scale and heterogeneity associated with enclosure studies (Frost et al. 1988), they frequently lack reference or adequate control treatments (Hurlbert 1984; Carpenter 1989). Also, because most independent variables cannot be regulated in field experiments, it is harder to obtain a reproducible result or to identify the explanation for a varying result (Diamond 1986). The present analyses suggest that combined interaction strength may have been weaker in large-scale studies, but the trends are not strong and the conservative conclusion is that successful application of biomanipulation is unrelated to size of the experimental study system.

Frost et al. (1988) believed that complex interactions in which fish are able to influence phytoplankton indirectly through increasing zooplankton mortality require a long time frame to become manifest. Mills and Forney (1988) considered it unfortunate that most of our knowledge of aquatic trophic dynamics arises from short-term manipulations, because such research (p. 26) "may have limited applicability to more mature ecosystems." Based on these comments, we might expect that if the predictions of top-down biomanipulation theory are true, a greater proportion of studies of increasingly longer duration should be expected to agree with the tenets of biomanipulation theory. Our analyses do not substantiate this hypothesis and the only trend that might be weakly detected is that long-term studies yield weaker interaction strengths. The question as to whether any of these perturbed systems have truly reached a stasis of equilibrium is important (Harris 1980; Thorp 1986).

Controversy exists with respect to the response pattern expected from either "press" or "pulse" (sensu Bender et al. 1984) trophic experiments, notwithstanding the basic rationale for undertaking these manipulation strategies to begin with. Frost et al. (1988) and Kitchell et al. (1988) considered pulse experiments adequate for achieving a response at the primary producer level and endorsed a "bold initial step" in terms of extreme fish manipulations. In contrast, Crowder et al. (1988) considered that because such experiments used unrealistic densities (e.g. fish vs. no fish; referred to as "sledgehammer manipulations") they may achieve (p. 151) "statistically significant results of little ecological significance" with interpretations being problematic at best. Because of this, Elser and Carpenter (1988) have suggested that only a sustained or long-term periodic fish manipulation could effectively biomanipulate and stabilize the trophic community. Our results indicate no tendency for effects to cascade down the trophic system in relation to increasing levels of fish manipulation.

McQueen et al. (1986), Vanni et al. (1990), and Lafontaine and McQueen (1991) have all suggested that top-down impacts may be stronger in oligotrophic systems than in eutrophic systems. Two mechanisms have been proposed to account for this effect. The first is that trophically induced shifts in fish community structure favor relatively higher piscivore-to-planktivore ratios and therefore more zooplankton and less phytoplankton (Persson et al. 1988). The second is that trophically induced shifts in phytoplankton biomass favor more ungrazable algae at higher nutrient concentrations (McQueen 1990). Our plot (Fig. 1) of mean interaction strength with respect to lake trophy (total P) fails to support any of these proposals.

Because they challenge theory tenacity, disconfirmatory syntheses such as the present study are crucial in preventing theories from "muddling along in a plausible but unconfirmed state" (Loehle 1987, p. 400). Theories, however, have a complex internal structure consisting of components such as concepts, definitions, and basic facts. For this reason, it is erroneous to believe that we can either accept or reject a theory as a complete unit (Loehle 1988). There is no doubt that negative interactions between trophic levels do exist and that they can be modulated by such variables as food-chain length and system productivity (Oksanen et al. 1981; McQueen et al. 1986; Persson et al. 1988). There is also no doubt that decreased planktivore biomass is sometimes associated with increased water clarity (McQueen et al. 1990), and nowhere is this more obvious than in complete fish removal experiments (Meijer et al. 1990).

But are these results due to top-down cascades and increased zooplankton grazing? The preceding analysis suggests that few are, and recent literature suggests that fish–phytoplankton interactions are confounded by many factors unrelated to zooplankton grazing. These include direct nutrient additions by fish (Vanni and Findlay 1990), direct nutrient additions by the small-bodied zooplankton associated with increased planktivore biomasses (Vanni and Findlay 1990), dead fish effects (Threlkeld 1988), bioturbation by fish (Meijer et al. 1990), and macrophyte shading, nutrient competition, and allelopathy (Moss 1990). There is generally a strong bottom-up relationship between nutrient availability and phytoplankton biomass, which suggests that until we understand more about the factors responsible for the disagreements between theory and results we must treat biomanipulation with caution. The prudent lake manager charged with the responsibility of reducing algal biomasses might be best advised to focus first on nutrient abatement and then on biomanipulation.

Espousal of any new theory requires a certain amount of evangelism on the part of those advocating its tenets (Loehle 1987). Dangers arise only when evangelism becomes supplanted by fundamentalism. Such a stage is characterized by a restriction of scientific vision and considerable resistance to paradigm change (Kuhn 1962). Theories must be judged by experience and rejected if they contradict accepted basic statements. Far from being "clearly confirmed" as Carpenter's introductory quote would have us believe, biomanipulation is truly at the stage of "paradigmal crisis" (Kuhn 1962). The discordant examples we have highlighted cannot be dismissed as being mere anomalies or issues of only scale, but rather call into question explicit and fundamental generalizations about biomanipulation theory itself. In this respect, we concur with studies that question the validity of the biomanipulation/cascading/top-down model (e.g. McQueen et al. 1989) and agree with Crowder et al. (1988) that support for the notion that piscivore effects ripple all the way down through the food web, influencing predation rates and biomasses at each level, is equivocal. For this reason we endorse Threlkeld's (1987, p. 171) call for "restraint in the application of the trophic-cascade concept to aquatic communities."

Science develops as the systematic presentation of immediate convictions determined through sense-perception (Popper 1968). This process operates best if approached phenomenologically, not fundamentally. Critical and unbiased examination of the complete data pool indicates that far too many unanswered questions remain to presently advocate biomanipulation as a justifiable management strategy for lake rehabilitation. Diagrams attractively portraying strong linkages between fish and phytoplankton biomasses, whether presented hierarchically (e.g. Kitchell et al. 1986) or as oscillating reciprocal sign waves (e.g. Christie et al. 1987; Int. Jt. Comm. 1988), are unfortunately largely idiographic. As the present review has shown, biomanipulation as a working theory has a long way to go before it can be accepted nomothetically (*see* Raup et al. 1973 or Loehle 1988). It is doubtful that this will happen for the simple reason that as a methodology, biomanipulation is based primarily on a concept of cascading negative trophic interactions. Such a view of the natural world is monistic, denying the operation of a plurality of variables (*see* Schoener 1986) which together function comprehensively in regulating food-web dynamics (Vadas 1989; McQueen et al. 1990).

Rita DeMelo
Robert France
Donald J. McQueen

Department of Biology
York University
4700 Keele St.
Toronto, Ontario M3J 1P3

References

ANDERSSON, G., H. BERGGREN, G. GRONBERG, AND C. GELIN. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia **59:** 9–15.

BENDER, E. A., T. J. CASE, AND M. E. GILPIN. 1984. Perturbation experiments in community ecology: Theory and practice. Ecology **65:** 1–13.

BENNDORF, J., H. KNESCHKE, K. KOSSATZ, AND E. PENZ. 1984. Manipulation of the pelagic food web by stocking with predacious fishes. Int. Rev. Gesamten Hydrobiol. **69:** 407–428.

———, AND OTHERS. 1988. Food-web manipulation by enhancement of piscivorous fish stocks: Long-term effects in the hypertrophic Bautzen Reservoir. Limnologica **19:** 97–110.

CARPENTER, S. R. 1988. Transmission of variance through lake food webs, p. 119–138. *In* S. Carpenter [ed.], Complex interactions in lake communities. Springer.

———. 1989. Replication and treatment strength in whole-lake experiments. Ecology **70:** 453–463.

———, AND J. F. KITCHELL. 1988. Consumer control of lake productivity. BioScience **38:** 764–769.

———, ———, AND J. R. HODGSON. 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634–638.

———, AND OTHERS. 1987. Regulation of lake primary productivity by food web structure. Ecology 68: 1863–1876.

CHRISTIE, W. J., AND OTHERS. 1987. A perspective on Great Lakes fish community rehabilitation. Can. J. Fish. Aquat. Sci. 44: 486–499.

CROWDER, L. B., AND OTHERS. 1988. Food web interaction in lakes, p. 141–160. *In* S. R. Carpenter [ed.], Complex interactions in lake communities. Springer.

DIAMOND, J. 1986. Overview: Laboratory experiments, field experiments, and natural experiments, p. 3–22. *In* J. Diamond and T. J. Case [eds.], Community ecology. Harper and Row.

DRENNER, R. W., S. T. THRELKELD, AND M. D. MCCRACKEN. 1986. Experimental analysis of the direct and indirect effects of an omnivorous filter-feeding clupeid on plankton community structure. Can. J. Fish. Aquat. Sci. 43: 1935–1945.

EDMONDSON, W. T., AND A. H. LITT. 1982. *Daphnia* in Lake Washington. Limnol. Oceanogr. 27: 272–293.

ELSER, J. J., AND S. R. CARPENTER. 1988. Predation-driven dynamics of zooplankton and phytoplankton communities in a whole-lake experiment. Oecologia 76: 148–154.

FEYERABEND, P. 1988. Against method. Verso.

FOTT, J., L. PECHAR, AND M. PRAZAKOVA. 1980. Fish as a factor controlling water quality in ponds, p. 225–261. *In* J. Barica and L. R. Mur [eds.], Hypertrophic ecosystems. Junk.

FROST, T. M., D. L. DEANGELIS, S. M. BARTELL, D. J. HALL, AND S. H. HURLBERT. 1988. Scale in the design and interpretation of aquatic community research, p. 229–260. *In* S. Carpenter [ed.], Complex interactions in lake communities. Springer.

GOAD, J. A. 1984. A biomanipulation experiment in Green Lake, Seattle, Washington. Arch. Hydrobiol. 102: 137–153.

GOPHEN, M. 1984. The impact of zooplankton status on the management of Lake Kinneret (Israel). Hydrobiologia 113: 249–258.

———. 1985*a*. Effects of fish predation on size class distribution of cladocerans in Lake Kinneret. Int. Ver. Theor. Angew. Limnol. Verh. 22: 3104–3108.

———. 1985*b*. The management of Lake Kinneret and its drainage basin, p. 127–138. *In* Scientific basis for water resources management. Proc. Symp., IAHS Publ. 153.

———, S. SERRUYA, AND S. THRELKELD. 1990. Long term patterns in nutrients, phytoplankton and zooplankton of Lake Kinneret and future predictions for ecosystem structure. Arch. Hydrobiol. 118: 449–460.

GRYGIEREK, E., A. HILLBRICHT-ILKOWSKA, AND I. SPODNIEWSKA. 1966. The effect of fish on plankton community in ponds. Int. Ver. Theor. Angew. Limnol. Verh. 16: 1359–1366.

HALL, D. J., W. E. COOPER, AND E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839–928.

HAMBRIGHT, K. D., R. J. TREBATOSKI, R. W. DRENNER, AND D. KETTLE. 1986. Experimental study of the impacts of bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) on pond community structure. Can. J. Fish. Aquat. Sci. 43: 1171–1176.

HANEY, J. 1987. Field studies on zooplankton-cyanobacteria interactions. N. Z. J. Mar. Freshwater Res. 21: 467–475.

HARRIS, G. P. 1980. Temporal and spatial scales in phytoplankton ecology: Mechanisms, methods, models, and management. Can. J. Fish. Aquat. Sci. 37: 877–900.

HENRIKSON, L., H. G. NYMAN, H. G. OSCARSON, AND J. A. E. STENSON. 1980. Trophic changes without changes in the external nutrient loading. Hydrobiologia 68: 257–263.

HILLBRICHT-ILKOWSKA, A., AND T. WEGLENSKA. 1978. Experimentally increased fish stock in the pond type Lake Warniak. 7. Numbers, biomass and production of zooplankton. Ekol. Pol. 21: 533–551.

HRBÁČEK, J., O. ALBERTOVÁ, B. DESORTOVÁ, V. GOTTWALDOVÁ, AND J. POPOVSKÝ. 1986. Relation of the zooplankton biomass and share of large cladocerans to the concentration of total phosphorous, chlorophyll-*a* and transparency in Hubenov and Vrchlice reservoirs. Limnologica 17: 301–308.

———, B. DESORTOVÁ, AND J. POPOVSKÝ. 1978. Influence of the fish stock on the phosphorous-chlorophyll ratio. Int. Ver. Theor. Angew. Limnol. Verh. 20: 1624–1628.

———, M. DVOŘÁKOVÁ, V. KOŘÍNEK, AND L. PROCHÁZKÓVA. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Int. Ver. Theor. Angew. Limnol. Verh. 14: 192–195.

HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187–211.

———, AND M. S. MULLA. 1981. Impacts of mosquitofish (*Gambusia affinis*) predation on plankton communities. Hydrobiologia 83: 125–151.

———, J. ZEDLER, AND D. FAIRBANKS. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. Nature 175: 639–641.

INTERNATIONAL JOINT COMMISSION. 1988. Rehabilitation of Lake Ontario: The role of nutrient reduction and food web dynamics. Great Lakes Sci. Advisory Bd.

KITCHELL, J. F., AND OTHERS. 1988. Epistemology, experiments, and pragmatism, p. 263–280. *In* S. Carpenter [ed.], Complex interactions in lake communities. Springer.

———, M. S. EVANS, D. SCAVIA, AND L. B. CROWDER. 1986. Food web regulation of water quality in Lake Michigan, p. 25–33. *In* Rehabilitation of Lake Ontario: The role of nutrient reduction and food web dynamics. Int. Jt. Comm. Rep. Great Lakes Sci. Advisory Bd.

KOKSVIK, J. I., AND A. LANGELAND. 1987. Effects of size selective predation by whitefish (*Coregonus lavaretus*) on *Daphnia galeata* Sars and *Cyclops scutifer* Sars in limnocorral experiments. Pol. Arch. Hydrobiol. 34: 67–80.

KOMARKOVA, J., R. FAINA, AND J. PARIZEK. 1986. Influence of the watershed and the fish stock upon the fish pond biocenoses. Limnologica **17:** 335–354.

KUHN, T. S. 1962. The structure of scientific revolutions. Univ. Chicago.

LAFONTAINE, N., AND D. J. MCQUEEN. 1991. Contrasting trophic level interactions in Lake St. George and Haynes Lake (Ontario) Canada. Can. J. Fish. Aquat. Sci. **48:** 356–363.

LAMMENS, E.H.R.R. 1988. Trophic interactions in the hypertrophic Lake Tjeukemeer: Top-down and bottom-up effects in relation to hydrology, predation and bioturbation during the period 1974–1985. Limnologica **19:** 81–85.

LANGELAND, A., J. I. KOKSVIK, Y. OLSEN, AND H. REINERTSEN. 1987. Limnocorral experiments in a eutrophic lake—effects of fish on the planktonic and chemical conditions. Pol. Arch. Hydrobiol. **34:** 51–65.

LEAH, R. T., B. MOSS, AND D. E. FORREST. 1980. The role of predation in causing major changes in the limnology of a hyper-eutrophic lake. Int. Rev. Gesamten Hydrobiol. **65:** 223–247.

LEHMAN, J. T. 1988. Algal biomass unaltered by food-web changes in Lake Michigan. Nature **332:** 537–538.

LEVINS, R. 1966. The strategy of model building in population biology. Am. Sci. **54:** 421–431.

LEVITAN, C., W. C. KERFOOT, AND W. R. DEMOTT. 1985. Ability of *Daphnia* to buffer trout lakes against periodic nutrient inputs. Int. Ver. Theor. Angew. Limnol. Verh. **22:** 3076–3082.

LOEHLE, C. 1987. Hypothesis testing in ecology: Psychological aspects and the importance of theory maturation. Q. Rev. Biol. **62:** 397–409.

———. 1988. Philosophical tools: Potential contributions to ecology. Oikos **51:** 97–104.

LOSOS, B., AND J. HETESA. 1973. The effect of mineral fertilization of carp fry on the composition and dynamics of plankton. Hydrobiol. Stud. **33:** 173–217.

LYNCH, M. 1979. Predation, competition, and zooplankton community structure: An experimental study. Limnol. Oceanogr. **24:** 253–272.

———, AND J. SHAPIRO. 1981. Predation, enrichment, and phytoplankton community structure. Limnol. Oceanogr. **26:** 86–102.

MCINTOSH, R. P. 1980. The background and some current problems of theoretical ecology. Synthese **43:** 195–255.

MCQUEEN, D. J. 1990. Manipulating lake community structure. Where do we go from here? Freshwater Biol. **23:** 613–620.

———, AND OTHERS. 1990. Effects of planktivore abundance on chlorophyll-*a* and Secchi depth. Hydrobiologia **200/201:** 337–341.

———, M. R. S. JOHANNES, J. R. POST, T. J. STEWART, AND D. R. S. LEAN. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. **59:** 289–309.

———, AND J. R. POST. 1986. Enclosure experiments: The effects of planktivorous fish, p. 313–318. *In* Lake and reservoir management. V. 2. Proc. 5th Int. Symp. Appl. Lake Watershed Manage. (NALMS).

———, AND ———. 1988. Cascading trophic interactions: Uncoupling at the zooplankton-phytoplankton link. Hydrobiologia **159:** 277–296.

———, ———, AND E. L. MILLS. 1986. Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci. **43:** 1571–1581.

MEIJER, M.-L., M. W. DE HAAN, A. W. BREUKELAAR, AND H. BUITEVELD. 1990. Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? Hydrobiologia **200/201:** 303–315.

MILLS, E. L., AND J. L. FORNEY. 1988. Trophic dynamics and development of pelagic food webs, p. 14–27. *In* S. Carpenter [ed.], Complex interactions in lake communities. Springer.

———, ———, AND K. J. WAGNER. 1987. Fish predation and its cascading effect on the Oneida Lake food chain, p. 118–131. *In* W. C. Kerfoot and A. Sih [eds.], Predation: Direct and indirect impacts on aquatic communities. New England.

MOSS B. 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia **200/201:** 367–377.

OKSANEN, L., S. D. FRETWELL, J. A. ARRUDA, AND P. NIEMELA. 1981. Exploitation ecosystems in gradients of primary productivity. Am. Nat. **118:** 240–261.

OLRIK, K., S. LUNDOER, AND K. RASMUSSEN. 1984. Interactions between phytoplankton, zooplankton and fish in the nutrient rich shallow Lake Hjarbaek Fjord, Denmark. Int. Rev. Gesamten Hydrobiol. **69:** 389–405.

PERSSON, L., G. ANDERSSON, S. F. HAMRIN, AND L. JOHANSSON. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems, p. 53–59. *In* S. Carpenter [ed.], Complex interactions in lake communities. Springer.

POPPER, K. R. 1968. The logic of scientific discovery. Harper and Row.

POST, J. R., AND D. J. MCQUEEN. 1987. The impact of planktivorous fish on the structure of a plankton community. Freshwater Biol. **17:** 79–89.

RANTA, E., S. HALLFORS, V. NUUTINEN, G. HALLFORS, AND K. KIVI. 1987. A field manipulation of trophic interactions in rock-pool plankton. Oikos **50:** 336–346.

RAUP, D. M., S. J. GOULD, T. J. M. SCHOPF, AND D. SIMBERLOFF. 1973. Stochastic models of phylogeny and the evolution of diversity. J. Geol. **81:** 525–542.

REINERTSEN, H., A. JENSEN, A. LANGELAND, AND Y. OLSEN. 1986. Algal competition for phosphorus: The influence of zooplankton and fish. Can. J. Fish. Aquat. Sci. **43:** 1135–1141.

———, AND Y. OLSEN. 1984. Effects of fish elimination on the phytoplankton community of a eutrophic lake. Int. Ver. Theor. Angew. Limnol. Verh. **22:** 649–657.

SCAVIA, D., G. L. FAHNENSTIEL, M. S. EVANS, D. J.

JUDE, AND J. T. LEHMAN. 1986. Influence of salmonine predation and weather on long-term water quality trends in Lake Michigan. Can. J. Fish. Aquat. Sci. **43:** 435–443.

SCHOENER, T. W. 1986. Overview: Kinds of ecological communities—ecology becomes pluralistic, p. 467–479. *In* J. Diamond and T. J. Case [eds.], Community ecology. Harper and Row.

SHAPIRO, J., AND D. I. WRIGHT. 1984. Lake restoration by biomanipulations. Round Lake, Minnesota—the first two years. Freshwater Biol. **14:** 371–383.

SIH, A. C. 1988. Complex interactions in benthic and littoral communities. Bull. Ecol. Soc. Am. **69:** 226–228.

SPENCER, C. N., AND D. L. KING. 1984. Role of fish in regulation of plant and animal communities in eutrophic ponds. Can. J. Fish. Aquat. Sci. **41:** 1851–1855.

SPILLER, D. A., AND T. SCHOENER. 1990. A terrestrial field experiment showing the impact of elimination of top predators on foliage damage. Nature **347:** 469–472.

SPODNIEWSKA, I., AND A. HILLBRICHT-ILKOWSKA. 1978. Experimentally increased fish stock in the pond type Lake Warniak. 6. Biomass and production of phytoplankton. Ekol. Pol. **21:** 519–532.

STENSETH, N. C. 1983. Grasses, grazers, mutualism and coevolution: A comment about handwaving in ecology. Oikos **41:** 152–153.

STENSON, J. A. E., AND OTHERS. 1978. Effects of fish removal from a small lake. Int. Ver. Theor. Angew. Limnol. Verh. **20:** 794–801.

STEVENS, W. K. 1990. Theory on the number of links in foodchain is upheld in river test. New York Times 11 Dec., p. C4.

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

THRELKELD, S. T. 1987. Experimental evaluation of trophic-cascade and nutrient-mediated effects of planktivorous fish on plankton community structure, p. 161–173. *In* W. C. Kerfoot and A. Sih [eds.], Predation: Direct and indirect impacts on aquatic communities. New England.

———. 1988. Planktivory and planktivore biomass effects on zooplankton, phytoplankton, and the trophic cascade. Limnol. Oceanogr. **33:** 1362–1375.

———, AND R. W. DRENNER. 1987. An experimental mesocosm study of residual and contemporary effects of an omnivorous, filter-feeding, clupeid fish on plankton community structure. Limnol. Oceanogr. **32:** 1331–1341.

TOWNSEND, C. 1988. Fish, fleas and phytoplankton. New Sci. **1617:** 67–70.

VADAS, R. L., JR. 1989. Food web patterns in ecosystems: A reply to Fretwell and Oksanen. Oikos **56:** 339–343.

VANNI, M. J. 1987*a*. Effects of food availability and fish predation on a zooplankton community. Ecol. Monogr. **57:** 61–88.

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

———, AND D. L. FINDLAY. 1990. Trophic cascades and phytoplankton community structure. Ecology **71:** 921–937.

———, C. LUECKE, J. F. KITCHELL, AND J. J. MAGNUSON. 1990. Food web effects on phytoplankton in Lake Mendota, Wisconsin, USA: Effects of massive fish mortality. Hydrobiologia **200/201:** 329–336.

VIJVERBERG, J., AND W. L. T. VAN DENSEN. 1984. The role of the fish in the food web of Tjeukemeer, The Netherlands. Int. Ver. Theor. Angew. Limnol. Verh. **22:** 891–896.

WAGNER, K. J. 1986. Biological management of a pond ecosystem to meet water use objectives, p. 54–59. *In* Lake and reservoir management. V. 2. Proc. 5th Int. Symp. Appl. Lake Watershed Manage. (NALMS).

WIENS, J. A., J. F. ADDICOTT, T. J. CASE, AND J. DIAMOND. 1986. Overview: The importance of spatial and temporal scale in ecological investigations, p. 145–153. *In* J. Diamond and T. J. Case [eds.], Community ecology. Harper and Row.