Biomanipulation: Hit or myth?1

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 enshrined 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 enshrined, 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 over extrapolation 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-

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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>
<thead>
<tr>
<th>Study</th>
<th>Name and location of lake or pond</th>
<th>Trophic status*</th>
<th>Total P (μg liter⁻¹)</th>
<th>Surface area (ha)</th>
<th>Mean depth (m)</th>
<th>Max depth (m)</th>
<th>Native fish species</th>
<th>Stocking rate</th>
<th>P loading</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hrbáček et al. 1961</td>
<td>Poltruba, Czechoslovakia</td>
<td>—</td>
<td>150</td>
<td>0.18</td>
<td>2.77</td>
<td>5.56</td>
<td>Various</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Grygierek et al. 1966</td>
<td>Manmade ponds, Poland</td>
<td>—</td>
<td>—</td>
<td>0.2</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Hall et al. 1970</td>
<td>Ponds, Cornell Univ., N.Y.</td>
<td>—</td>
<td>17 (1966)–64 (1965)</td>
<td>0.07</td>
<td>—</td>
<td>1.3</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Losos and Hetesa 1973</td>
<td>Ponds, state fishery, Poland</td>
<td>—</td>
<td>0.05</td>
<td>0.12</td>
<td>0.15</td>
<td>—</td>
<td>—</td>
<td>50 kg ha⁻¹</td>
<td>—</td>
</tr>
<tr>
<td>Hrbáček et al. 1978; Hrbáček et al. 1986</td>
<td>Hubenov and Vrchlice Reservoirs, Czechoslovakia</td>
<td>E</td>
<td>30 mg m⁻³</td>
<td>0.516; 0.925</td>
<td>8.93</td>
<td>31.5</td>
<td>Brown trout, rainbow trout; roach, perch, cyprinids</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Spodniewska and Hillbricht-Iiikowska 1978; Hillbricht-Iiikowska and Wegienska 1978</td>
<td>Lake Warniak, Poland</td>
<td>E</td>
<td>—</td>
<td>38.4</td>
<td>1.5</td>
<td>3.7</td>
<td>Carp, bream</td>
<td>893 kg carp, 849 kg bream</td>
<td>—</td>
</tr>
<tr>
<td>Stenson et al. 1978; Henrikson et al. 1980</td>
<td>Lilla, Stockelidsvatten, Behuslan, Sweden</td>
<td>O</td>
<td>—</td>
<td>1</td>
<td>—</td>
<td>8</td>
<td>Roach</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Fott et al. 1980</td>
<td>Velký Pálenec, Czechoslovakia</td>
<td>E</td>
<td>—</td>
<td>31</td>
<td>1.4</td>
<td>—</td>
<td>Carp, whitefish</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Leah et al. 1980</td>
<td>River Yare, Brundall, U.K.</td>
<td>H</td>
<td>2,000 (summer)</td>
<td>—</td>
<td>1.2</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Lynch 1979; Lynch and Shapiro 1981</td>
<td>Pleasant Pond, Minn.</td>
<td>—</td>
<td>—</td>
<td>0.25</td>
<td>2.5</td>
<td>—</td>
<td>Fathead minnows</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Benndorf et al. 1984</td>
<td>Flooded quarry, Germany</td>
<td>M</td>
<td>—</td>
<td>0.044</td>
<td>7</td>
<td>—</td>
<td>Various</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Gophen 1984, 1985a,b</td>
<td>Lake Kinneret, Israel</td>
<td>E</td>
<td>12</td>
<td>25,200</td>
<td>24</td>
<td>42</td>
<td>Various</td>
<td>107 t yr⁻¹ TP</td>
<td>—</td>
</tr>
<tr>
<td>Olrik et al. 1984</td>
<td>Lake Hjarbaek Fjord, Denmark</td>
<td>H</td>
<td>300</td>
<td>2.4</td>
<td>2</td>
<td>—</td>
<td>Various</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Reinertsen and Olsen 1984</td>
<td>Haugatjern, Norway</td>
<td>E</td>
<td>15</td>
<td>9.1</td>
<td>7.6</td>
<td>15.5</td>
<td>Whitefish, perch</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Shapiro and Wright 1984</td>
<td>Round Lake, Minn.</td>
<td>E</td>
<td>47.8</td>
<td>12.6</td>
<td>2.9</td>
<td>10.5</td>
<td>Various</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>
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 × 10⁶         | 84            | 285           | Various             | 7.4–16 × 10⁶ 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, Minus 90% bass, plus 44,901 minnows | —              |
| Carpenter et al. 1987        | Peter Lake, Mich.                | O               | 2.4                  | 8.3               | 19.3          | —             | —                   | —             | —              |
| 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 × 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—meso-eutrophic; 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: —.)

<table>
<thead>
<tr>
<th>Study</th>
<th>Method</th>
<th>Duration</th>
<th>Fish species</th>
<th>Stocking rate</th>
<th>Nutrient loading</th>
<th>Observed responses between trophic levels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hrbaček et al. 1961</td>
<td>Rotenone</td>
<td>Apr–Oct 57</td>
<td></td>
<td></td>
<td></td>
<td>I D Y Y Y</td>
</tr>
<tr>
<td>Grygierek et al. 1966</td>
<td>Stocking</td>
<td>1957–1961</td>
<td>Carp fry</td>
<td>12.5–150 kg ha⁻¹</td>
<td></td>
<td>I N U</td>
</tr>
<tr>
<td>Hall et al. 1970</td>
<td>Stocking and nutrient enrichment</td>
<td>Jun–Oct 67</td>
<td>Bluegill sunfish</td>
<td>47 kg ha⁻¹</td>
<td>0–272 kg week⁻¹ fertilizer</td>
<td>I Y N</td>
</tr>
<tr>
<td>Losos and Heta 1973</td>
<td>Stocking and nutrient enrichment</td>
<td>Jul–Aug 63, 64</td>
<td>Carp fry</td>
<td>38.4 kg ha⁻¹ (1963), 9.6 kg ha⁻¹ (1964)</td>
<td>300–600 kg ha⁻¹ fertilizer</td>
<td>I Y Y Y</td>
</tr>
<tr>
<td>Spodniewska and Hillbricht-Ilkowska 1978;</td>
<td>Sampling</td>
<td>Apr–Oct 67–69</td>
<td></td>
<td></td>
<td></td>
<td>I Y N</td>
</tr>
<tr>
<td>Hillbricht-Ilkowska and Weglenika 1978</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fott et al. 1980</td>
<td>Sampling</td>
<td>May, Aug–Sep 75–79</td>
<td></td>
<td>Up to 1,880 kg ha⁻¹ carp and 60 kg ha⁻¹ whitefish</td>
<td></td>
<td>I Y U U</td>
</tr>
<tr>
<td>Edmondson and Litt 1982</td>
<td>Sampling</td>
<td>1971–1980</td>
<td></td>
<td></td>
<td></td>
<td>Low N* N* N*</td>
</tr>
<tr>
<td>Lynch 1979; Lynch and Shapiro 1981</td>
<td>Sampling</td>
<td>Apr–Aug 76</td>
<td>Fathead minnows</td>
<td></td>
<td></td>
<td>I Y U</td>
</tr>
</tbody>
</table>
Table 2. Continued.

<table>
<thead>
<tr>
<th>Study</th>
<th>Method</th>
<th>Manipulation</th>
<th>Observed responses between trophic levels</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Duration</td>
<td>Fish species</td>
</tr>
<tr>
<td>Olrik et al. 1984</td>
<td>Sampling</td>
<td>Mar–Oct 81</td>
<td>—</td>
</tr>
<tr>
<td>Shapiro and Wright 1984</td>
<td>Rotenone and restocking</td>
<td>1980–1982</td>
<td>Bass, walleye, bluegill</td>
</tr>
<tr>
<td>Spencer and King 1984</td>
<td>Sampling</td>
<td>Jun–Nov 79</td>
<td>Fathead minnows, brook sticklebacks</td>
</tr>
<tr>
<td>Komarkova et al. 1986</td>
<td>Sampling</td>
<td>Apr–Aug 76–78</td>
<td>—</td>
</tr>
<tr>
<td>Carpenter et al. 1987</td>
<td>Piscivore stocking and plankt. removal</td>
<td>Jun–Sep 80</td>
<td>Largemouth bass, minnows</td>
</tr>
<tr>
<td>Carpenter et al. 1987</td>
<td>Piscivore removal and plankt. stocking</td>
<td>Jun–Sep 80</td>
<td>Largemouth bass, minnows</td>
</tr>
<tr>
<td></td>
<td>Two pools separation and stocking</td>
<td>1978 d</td>
<td>Tench</td>
</tr>
<tr>
<td>Benndorf et al. 1984, 1988</td>
<td>Catch restriction and stocking</td>
<td>1977–1985</td>
<td>Perch, pikeperch</td>
</tr>
<tr>
<td>McQueen et al. 1989</td>
<td>Sampling</td>
<td>1980–1986</td>
<td>—</td>
</tr>
</tbody>
</table>

* 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.

<table>
<thead>
<tr>
<th>Study</th>
<th>Surface area (ha)</th>
<th>Duration</th>
<th>Fish species</th>
<th>Stocking rate</th>
<th>Nutrient loading</th>
<th>Total P (µg liter⁻¹)</th>
<th>Observed responses between trophic levels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hurlbert et al. 1972</td>
<td>0.0012</td>
<td>1970–1971</td>
<td><em>Gambusia affinis</em></td>
<td>50 fish pond⁻¹</td>
<td>—</td>
<td>—</td>
<td>I Y U U</td>
</tr>
<tr>
<td>Andersson et al. 1978</td>
<td>0.0007</td>
<td>Jun–Oct 76</td>
<td>Bream, roach, crucian carp</td>
<td>90 and 220 g m⁻²</td>
<td>—</td>
<td>359</td>
<td>I U U U</td>
</tr>
<tr>
<td>Lynch 1979; Lynch and Shapiro 1981</td>
<td>0.78 × 10⁻⁵</td>
<td>40 d, 1975</td>
<td>Bluegill sunfish</td>
<td>100–1,064 kg ha⁻¹</td>
<td>—</td>
<td>109</td>
<td>I Y Y —</td>
</tr>
<tr>
<td>Hurlbert and Mulla 1981</td>
<td>0.0024</td>
<td>Aug 67–May 68</td>
<td><em>G. affinis</em></td>
<td>50–450 fish pond⁻¹</td>
<td>—</td>
<td>—</td>
<td>I Y Y —</td>
</tr>
<tr>
<td>Goad 1984</td>
<td>0.0003</td>
<td>15 d, 1981</td>
<td>Perch, trout</td>
<td>5–50 and 20 g m⁻²</td>
<td>—</td>
<td>—</td>
<td>I U U —</td>
</tr>
<tr>
<td>Levitan et al. 1985</td>
<td>0.0003</td>
<td>1979–1980</td>
<td>Creek chubs, trout</td>
<td>6 chubs, 8 trout</td>
<td>1.6–16 µM P, 25–250 µM N</td>
<td>29</td>
<td>I Y Y —</td>
</tr>
<tr>
<td>Drenner et al. 1986</td>
<td>0.0004</td>
<td>Nov 82, Mar, Jun, Sep 83 (45–53 d)</td>
<td><em>Dorosoma, Menidia</em></td>
<td>0–271.2 and 0–19.1 g</td>
<td>—</td>
<td>7.8 (SRP)</td>
<td>I Y N N</td>
</tr>
<tr>
<td>Hambright et al. 1986</td>
<td>0.006</td>
<td>5 Jun–30 Sep 85</td>
<td>Bluegill, large-mouth bass Various</td>
<td>280 and 112 kg ha⁻¹, 1,363 kg ha⁻¹</td>
<td>—</td>
<td>46</td>
<td>I Y Y U</td>
</tr>
<tr>
<td>McQueen and Post 1986</td>
<td>0.005</td>
<td>Summer 1983–1985</td>
<td>Various</td>
<td>—</td>
<td>—</td>
<td>50</td>
<td>D U Y —</td>
</tr>
<tr>
<td>McQueen and Post 1986</td>
<td>0.02</td>
<td>May–Sep 82</td>
<td>0+ yellow perch</td>
<td>0, 200, 600 fish</td>
<td>5 g 90% H₃PO₄, 125 g NaNO₃</td>
<td>50</td>
<td>I U U —</td>
</tr>
<tr>
<td>Reinertsen et al. 1986</td>
<td>0.00018</td>
<td>Aug 79–Jun 80</td>
<td>0+ perch, whitefish</td>
<td>800 kg ha⁻¹</td>
<td>—</td>
<td>15</td>
<td>I Y U —</td>
</tr>
<tr>
<td>Koksvik and Langeland 1987; Langeland et al. 1987</td>
<td>0.0019</td>
<td>5 Jun–30 Sep 80</td>
<td>Whitefish</td>
<td>640–700 kg ha⁻¹</td>
<td>—</td>
<td>7.6</td>
<td>I Y U N</td>
</tr>
<tr>
<td>McQueen and Post 1988</td>
<td>0.005</td>
<td>7 Jun–25 Oct 85</td>
<td>0+ yellow perch</td>
<td>50 enclosure⁻¹</td>
<td>—</td>
<td>—</td>
<td>I Y N N</td>
</tr>
<tr>
<td>Post and McQueen 1987</td>
<td>0.005</td>
<td>2 Jun–27 Sep 82</td>
<td>0+ yellow perch</td>
<td>2–5 kg ha⁻¹</td>
<td>5 g P; 126 g N</td>
<td>—</td>
<td>I Y N Y</td>
</tr>
<tr>
<td>Study</td>
<td>Surface area (ha)</td>
<td>Duration</td>
<td>Fish species</td>
<td>Stocking rate</td>
<td>Nutrient loading</td>
<td>Total P (µg liter⁻¹)</td>
<td>Observed responses between trophic levels</td>
</tr>
<tr>
<td>-----------------------------</td>
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<td>------------------------------------------</td>
</tr>
<tr>
<td>Threlkeld 1987, 1988</td>
<td>0.0004</td>
<td>(1987) May–Nov 84</td>
<td><em>Menidia, Tilapia, Dorosoma</em></td>
<td>350 g wet wt</td>
<td>–</td>
<td>–</td>
<td>– I Y N* N*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1988) May–Dec 85; Mar–May 86</td>
<td><em>Menidia</em></td>
<td>0–256 tank⁻¹</td>
<td>0–32 dead fish tank⁻¹</td>
<td>–</td>
<td>– I Y N* N*</td>
</tr>
<tr>
<td>Threlkeld and Drenner 1987</td>
<td>0.0004</td>
<td>271 d</td>
<td><em>Dorosoma</em></td>
<td>0–249.3 g</td>
<td>–</td>
<td>5.754</td>
<td>– I U U U</td>
</tr>
<tr>
<td>Threlkeld and Drenner 1987</td>
<td>0.0004</td>
<td>271 d</td>
<td><em>Menidia, Dorosoma</em></td>
<td>0–19.3 and 0–272.3 g</td>
<td>–</td>
<td>5.754</td>
<td>– I Y U U</td>
</tr>
<tr>
<td>Vanni 1987a,b</td>
<td>0.00019</td>
<td>Jul–Aug 80, 81</td>
<td>Bluegill sunfish (1980–2 enclosure⁻¹)</td>
<td>1</td>
<td>0–10 µg liter⁻¹</td>
<td>–</td>
<td>– I Y U –</td>
</tr>
</tbody>
</table>

Details in Table 4.*

*Plankton interactions are due to plankton growth from indirect nutrient ad-
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.

Goa 1984: Noted that Chl a concentrations in the fish and fish-free enclosures were all similar (∼50 μg 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, 1985a,b; Gophen et al. 1990: Noted that potential effects of zooplankton on phytoplankton were confounded by changes in nutrient loading and N:P ratios.

Grygier 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 Vrhalice, but the differences were not significant. Also, higher Chl a values in Vrhalice 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 limnocoral 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 limnocoral. During spring and late summer Daphnia biomass was equal in both limnocorals. Staurastrum luetschemulleri increased during late July and August when Daphnia biomass was similar in both limnocorals. During midsummer, phytoplankton biomass was about equal in both limnocorals.

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 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 NH₃).

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.
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 absurdeness—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
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 ungrazeable 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 gen-
ernally a strong bottom-up relationship be-
tween nutrient availability and phytoplank-
ton biomass, which suggests that until we
understand more about the factors respon-
sible 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 cer-
tain amount of evangelism on the part of
those advocating its tenets (Loehle 1987).
Dangers arise only when evangelism be-
comes 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 Car-
penter's introductory quote would have us
believe, biomanipulation is truly at the stage
of "paradigmatic crisis" (Kuhn 1962). The
discordant examples we have highlighted
cannot be dismissed as being mere anom-
alies or issues of only scale, but rather call
into question explicit and fundamental gen-
eralizations about biomanipulation theory
itself. In this respect, we concur with studies
that question the validity of the biomanipu-
lation/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 pre-
sentation of immediate convictions deter-
mined through sense-perception (Popper
1968). This process operates best if ap-
proached phenomenologically, not funda-
mentally. Critical and unbiased examina-
tion of the complete data pool indicates that
far too many unanswered questions remain
to presently advocate biomanipulation as a
justifiable management strategy for lake re-
habilitation. Diagrams attractively portray-
ing strong linkages between fish and phy-
toplankton biomasses, whether presented
 hierarchically (e.g. Kitchell et al. 1986) or
as oscillating reciprocal sign waves (e.g.
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, biomanipu-
lation is based primarily on a concept of
cascading negative trophic interactions. Such
a view of the natural world is monistic, de-
nyng the operation of a plurality of vari-
ables (see Schoener 1986) which together
function comprehensively in regulating
food-web dynamics (Vadas 1989; McQueen
et al. 1990).

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