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A meta-analysis of the freshwater trophic cascade

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ABSTRACT The generality of the trophic cascade has been an intensely debated topic among ecologists. We conducted a meta-analysis of 54 separate enclosure and pond experiments that measured the response of the zooplankton and phytoplankton to zooplanktivorous fish treatments. These results provide unequivocal support for the trophic cascade hypothesis in freshwater food webs. Zooplanktivorous fish treatments resulted in reduced zooplankton biomass and increased phytoplankton biomass. The trophic cascade was weakly dampened at the level of the phytoplankton. However, the response of the phytoplankton to the trophic cascade was highly skewed, with very strong responses in slightly more than one-third of the cases and weak responses in the others.

Trophic cascade theory holds that each trophic level of a food web is inversely and directly related to trophic levels above and below it (1). For example, if the abundance of large piscivorous fish is increased in a lake, the abundance of their prey zooplanktivorous fish should decrease, large herbivorous zooplankton abundance should increase, and phytoplankton biomass should decrease. This theory has stimulated new research in many areas of ecology (2). Trophic cascade theory was generated from empirical observations that piscivorous fish can dramatically reduce populations of zooplanktivorous fish, zooplanktivorous fish can dramatically alter freshwater zooplankton communities, and zooplankton grazing can in turn have large impacts on phytoplankton communities (3–6).

Almost from its first presentation, this theory has been embroiled in a controversy over whether "top-down" (i.e., consumer) or "bottom-up" (i.e., nutrient) forces determine the structure of aquatic food webs (2, 7). Based on the observation that many studies do not show statistically significant impacts of piscivorous or zooplanktivorous fish on the structure of freshwater food webs, a recent critique of this theory argued that "even the briefest perusal of the pertinent literature indicates that, far from being robust, the trophic-cascade theory may be unsoundly based on many half-truths and much hand-waving and overextrapolation of the data" (8).

The critique of DeMelo *et al.* (8) of trophic cascade theory used a technique for summarizing information from the literature called vote counting. Vote counting consists of simply tallying all studies that detect statistically significant effects and nonsignificant effects, and inferring the generality of phenomenon (9–11). Although this technique is the most universal method of summarizing information from large bodies of literature in the ecological sciences, it has a major flaw in that it perpetuates all type II statistical errors (e.g., failing to detect a true effect) in the original studies. Because ecological field studies usually use small sample sizes and have high variability, they are particularly susceptible to type II errors (12, 13). We have analyzed the data from most of the studies cited by DeMelo *et al.* (8), as well as many other studies, using a statistical technique called meta-analysis. Meta-analysis is a simple and robust approach to detecting central tendencies in large multi-investigation data sets (9–11). By quantitatively summarizing and statistically testing information from many studies, this technique greatly reduces propagation of type II errors.

In a search of the literature, we located 34 published studies that reported on 54 separate enclosure and pond experiments examining zooplanktivorous fish impacts on zooplankton and phytoplankton communities. We have restricted our analysis to enclosure and experimental pond studies because relatively few whole-lake investigations have been reported in the literature (8) and meta-analysis is most powerful when a large number of studies are compared (9, 10). Furthermore, long-term monitoring has shown that tremendous variability in mean annual primary production in lakes can be due to serial autocorrelation, climatic impacts, and progressive eutrophication (14–16). This external variability is likely to obscure detection of a trophic cascade if only a small number of studies are compared. Similarly, this meta-analysis was not conducted on experiments examining piscivorous fish impacts on planktivorous fish, zooplankton and phytoplankton communities, because experiments employing this design are rare compared with the numbers of experiments employing zooplanktivorous fish treatments.

Of the 54 published investigations of zooplanktivorous fish impacts on zooplankton and phytoplankton communities 12 (17–25) were not replicated, 31 (26–42) were replicated but did not report the necessary measure of variability, and 11 (refs. 43–50, and M.T.B., unpublished data) were replicated and reported treatment means, variability, and sample size for both the zooplankton and phytoplankton. Due to the nature of the available data we conducted two data analyses. The first was an analysis of the mean responses to fish treatments across all 54 experiments (Fig. 1). The second was a full meta-analysis according to Gurevitch and Hedges (10) utilizing treatment responses, variability, and sample size information for the 11 fully replicated and reported investigations (Table 1).

The results of the data analysis employing all 54 enclosure experiments (Fig. 1) showed that in general the zooplanktivorous fish treatments resulted in greatly decreased zooplankton biomass; median = 29% of the control value. Similarly, the fish treatments resulted in increased phytoplankton biomass; median = 176% of control value. These results were strongly supported by a full meta-analysis of the 11 fully replicated and adequately reported experiments that showed that the fish treatments reduced zooplankton biomass by 1.4 SD and increased phytoplankton biomass by 2.0 SD (Table 1). The significant Q statistics of the full meta-analysis indicate that the zooplanktivorous fish treatments resulted in general response about which individual experiments varied significantly. That the results of individual experiments vary significantly is expected because the experiments summarized employed different treatment fish, different sized enclosures, and lasted varying lengths of time.

The results of these analyses (Fig. 1 and Table 1) provide unequivocal support for the trophic cascade hypothesis in freshwater planktonic ecosystems (1). These results should help resolve the debate (2, 8, 51) over whether the trophic cascade is a general feature of freshwater food webs and focus

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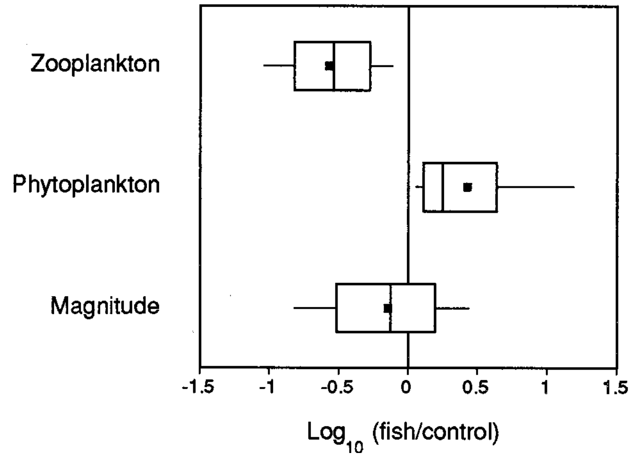

FIG. 1. Averaged responses of the zooplankton and phytoplankton to zooplanktivorous fish treatments for all 54 enclosure experiments. The line through the middle of the box shows the median and the solid square shows the mean of the distribution. The outer edges of the box correspond to the 25th and 75th percentiles and the "whiskers" to the 10th and 90th percentiles. Only studies that utilized concurrent zero fish controls were used. When multiple fish treatment levels were used we compared the high fish to the control treatments. We did not use data from any treatments where the authors reported significant mortality of treatment fish or where nutrients were added. For example, Threlkeld (30) reported on a series of experiments where many of the treatment fish died during the course of the experiment. In these experiments we compared the highest fish treatments that did not have high fish mortality to the fishless control treatment. These criteria meant we were not able to use several of Threlkeld's (30) experiments (e.g., experiments 2 and 5) in our analysis. The data from each experiment were "scaled" by dividing the mean values from the fish treatment by the corresponding control values. Total crustacean zooplankton biomass was used to characterize the response of the zooplankton; however, when this parameter was not presented we used total zooplankton biomass, crustacean abundance, or large crustacean biomass, etc. Similarly, chlorophyll concentration was preferentially used to characterize the phytoplankton response; however, in some cases phytoplankton biovolume, primary production, or fluorescence was used instead. Magnitude, a measure of whether the cascade is dampened or heightened at the phytoplankton level, was calculated by adding the $\log_{10}$ transformed phytoplankton response to the $\log_{10}$ transformed zooplankton response. If the response for the phytoplankton and zooplankton was of similar magnitude, then their log-transformed sum should be zero. The data were tested against a null hypothesis of no effect by comparing $\log_{10}$ transformed data (fish/control) against a hypothetical population mean = 0. The zooplanktivorous fish treatments resulted in greatly decreased zooplankton biomass (t value = -11.00, n = 54, $P < 0.0001$), and increased phytoplankton biomass (Wilcoxon sign-rank test, z = 5.11, n = 54, $P < 0.0001$). The magnitude of the phytoplankton response was weakly different from the hypothetical mean of zero (t value = -2.02, n = 54, P = 0.0485).

the attention of researchers on other questions, such as explaining variation in the response of phytoplankton to the cascade. In 52 of the 54 studies summarized by us zooplankton biomass was depressed by zooplanktivorous fish treatments, whereas in 51 of 54 cases these same treatments increased the biomass of the phytoplankton. However, in many cases, these effects were small, particularly for the phytoplankton, and would not be statistically detected by a study with no or few replicates and high variability. The lack of treatment effects noted by DeMelo *et al.* (8) appears to be mainly the result of low statistical power.

It should be noted, however, that enclosure experiments are not completely representative of lakes. Only a few studies employed enclosures that were open to the sediments and some planktivorous fish, in particular many Eurasian cyprinids, are known to actively stir up sediments. In addition, many of the analyzed experiments acknowledged that they used treatment fish abundances that were greater than those typically seen in the relevant lakes.

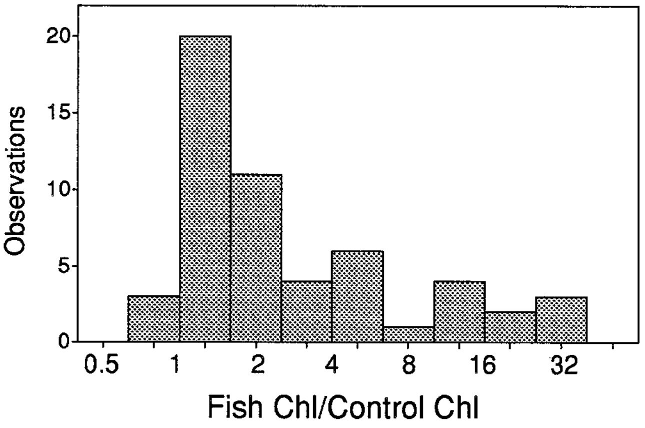

FIG. 2. The frequency distribution of the phytoplankton's response to the zooplanktivorous fish treatments. These values were computed as mean Fish Chl/mean Control Chl, with values greater than one indicating a positive response of the phytoplankton biomass to the fish treatments. This distribution has a skewness value of 2.59.

Our analysis (Fig. 1) indicates that the response of the phytoplankton to the cascade was weakly dampened with the magnitude of the phytoplankton's response 72% (median) of the magnitude of the zooplankton's response to the cascade. However, in 21 of the 54 cases, the phytoplankton's response was actually stronger than that observed for the zooplankton. Although these results do suggest that the cascade is somewhat dampened, they do not support McQueen's contention (52) that the trophic cascade is strongly dampened at the level of the phytoplankton. In fact, dampening was weak compared with the variability in the response of the phytoplankton to the cascade.

The phytoplankton's response to the zooplanktivorous fish treatments was highly skewed (Fig. 2). The median phytoplankton response was a 76% increase in biomass, whereas the geometric mean response was a 166% increase in biomass. The 34 cases where the phytoplankton showed the smallest response to the trophic cascade averaged (geometric mean) only a 38% increase in phytoplankton biomass, whereas the 20

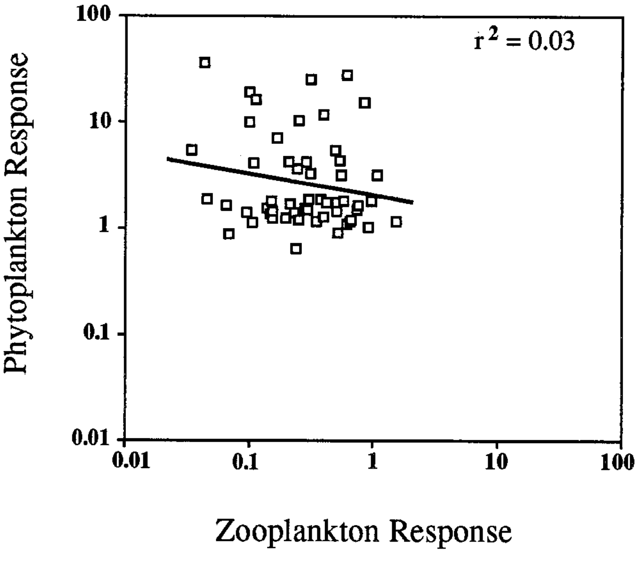

FIG. 3. The relationship between the response (Fish mean/Control mean) of the zooplankton to the response of the phytoplankton in the zooplanktivore experiments. This relationship was not significant (linear regression: r^2 = 0.032, F test = 1.70, n = 54, P = 0.20).

Table 1. Results of a full meta-analysis of the 11 fully replicated and reported enclosure and pond experiments according to Gurevitch and Hedges (10)

Publication	Fish species	Source	Parameter	Effect size, d	Variance, v	Weight, w	v*	w*
Zooplankton								
Hurlbert *et al.* (43)	Mosquitofish	Table 1	Crustacean biomass*	−2.37	1.14	0.88	1.50	0.66
Lynch (44)	Bluegill	Fig. 3	Crustacean biomass*	−0.64	0.56	1.79	0.93	1.08
Spencer and King (45)	Fathead minnow	Table 1	Crustacean biomass*	−2.05	1.52	0.66	1.88	0.53
Leibold (46)	Bluegill	Fig. 5	Crustacean biomass*	−1.54	1.30	0.77	1.62	0.62
Vanni and Findlay (47)	Yellow perch	Table 2	Crustacean biomass	−6.60	4.30	0.23	4.67	0.21
McQueen *et al.* (48)	Yellow perch	Fig. 3	Zooplankton biomass	0.26	1.01	0.99	1.38	0.73
Christoffersen (49)	Roach	Fig. 8	Crustacean biomass	−3.00	2.13	0.47	2.49	0.40
Hambright (50)	Fathead minnow	Fig. 3, 88	Crustacean biomass	−0.68	0.42	2.36	0.79	1.26
Hambright (50)	Fathead minnow	Fig. 3, 89	Crustacean biomass	−1.39	0.56	1.79	0.93	1.08
Hambright (50)	Fathead minnow	Fig. 3, 90	Crustacean biomass	−0.64	0.47	2.12	0.84	1.19
M.T.B., unpublished data	Golden shiner		Crustacean biomass	−3.88	1.92	0.52	2.29	0.44
Phytoplankton								
Hurlbert *et al.* (43)	Mosquitofish	Table 1	Coccochloris	10.61	10.06	0.10	10.30	0.10
Lynch (44)	Bluegill	Fig. 5	Biovolume	2.97	1.09	0.92	1.33	0.75
Spencer and King (45)	Fathead minnow	Table 1	Biovolume	1.58	1.31	0.76	1.56	0.64
Leibold (46)	Bluegill	Fig. 3	Chlorophyll	2.55	1.82	0.55	2.06	0.48
Vanni and Findlay (47)	Yellow perch	Table 3	Biovolume	5.67	3.35	0.30	3.59	0.28
McQueen *et al.* (48)	Yellow perch	Fig. 1	Chlorophyll	1.57	1.31	0.76	1.56	0.64
Christoffersen (49)	Roach	Fig. 8	Biovolume	3.04	2.16	0.46	2.41	0.42
Hambright (50)	Fathead minnow	Fig. 7, 88	Chlorophyll	0.65	0.42	2.37	0.67	1.50
Hambright (50)	Fathead minnow	Fig. 7, 89	Chlorophyll	2.55	0.81	1.23	1.06	0.95
Hambright (50)	Fathead minnow	Fig. 7, 90	Chlorophyll	1.05	0.51	1.96	0.76	1.32
M.T.B., unpublished data	Golden shiner		Chlorophyll	2.11	1.04	0.96	1.29	0.78

Summation of mixed model results

	Effect size, d+*	Variability, SD(d+*)	99.9% C.I., ±	Heterogeneity, Q
Zooplankton	−1.39	0.34	1.13	17.83
Phytoplankton	2.01	0.36	1.20	19.25

This analysis showed the average decrease in zooplankton biomass in the zooplanktivorous fish treatments was −1.39 standard deviations, whereas the average increase in phytoplankton biomass was 2.01 SD. The results for both the zooplankton and phytoplankton were highly statistically significant, i.e., the 99.9% confidence intervals did not overlap zero. The test of homogeneity (Q statistic which approximates a χ^2 distribution) between experiments was moderately significant ($P < 0.05$) for both the zooplankton and phytoplankton responses. This suggests that there is not a fixed average effect about which all results randomly vary, but instead suggests that there is a general response and real differences between experiments that are not solely due to random processes.

*Biomass estimated by assuming weights for specific taxa.

highest responses averaged a 711% increase in phytoplankton biomass. In short, in 63% of the cases, the impact of the trophic cascade on the phytoplankton was rather weak, whereas in 37% of the cases the impact on the phytoplankton was very strong.

Although we observed a wide range in the response of the zooplankton to the cascade, variability in the phytoplankton's response was not inversely associated with variability in the zooplankton's response (Fig. 3). This result is not consistent with some interpretations of trophic cascade theory. For example, Peters (53) suggests one can test the predictions of the trophic cascade theory by simply plotting the residuals of a chlorophyll-versus-nutrient regression against zooplankton biomass. Since several authors have done this and failed to obtain the expected strong negative relationship between unexplained variation in the phytoplankton community's response to lake nutrient levels and zooplankton biomass, Peters concludes (ref. 53, p. 144) "On this basis, the theory that top-down control influences chlorophyll development in lakes must be rejected." Our analysis indicates that one can obtain very strong agreement with the general features of the trophic cascade theory without obtaining a negative linear relationship between the responses of the phytoplankton and zooplankton. This also suggests one must reject Peters' rejection of the trophic cascade theory.

In some cases, small decreases in zooplankton biomass corresponded to large increases in phytoplankton biomass, whereas in other cases large decreases in the zooplankton corresponded to small increases in the phytoplankton. Dominance by large zooplankters like *Daphnia* may increase the impact of the zooplankton on the phytoplankton, and dominance by colonial cyanobacteria may minimize the phytoplankton's susceptibility to grazing by zooplankton. Unfortunately, most of the experiments reported in the present study did not present the composition of the zooplankton and phytoplankton communities in sufficient detail to make a comprehensive quantitative assessment of the role of the zooplankton and phytoplankton composition in determining the strength of the trophic cascade.

Although our results strongly support trophic cascade theory, they provide weaker support for the idea that manipulations of fish communities can be used to consistently control algal biomass in lakes (e.g., biomanipulation). That is, variation in the response of the phytoplankton to the trophic cascade suggests that there is an approximately 60% chance that even aggressive biomanipulation, through reductions in zooplanktivorous fish abundance, would result in only a minor reduction in phytoplankton biomass and an equally small increase in water clarity. The continuing challenge to aquatic food web researchers is understanding why the response of the phytoplankton to the trophic cascade is so variable.

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