Experimental Study of the Impacts of Bluegill (*Lepomis macrochirus*) and Largemouth Bass (*Micropterus salmoides*) on Pond Community Structure

K. David Hambright, Robert J. Trebatoski, and Ray W. Drenner

Department of Biology, Texas Christian University, Fort Worth, TX 76129, USA

and Dean Kettle

Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045, USA

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We examined community impacts of bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) in a summer experimental pond study of factorial design with four treatment combinations (fishless, bluegill, largemouth bass, and bluegill with largemouth bass). *Ceriodaphnia reticulata*, *Daphnia pulicaria*, *Chaoborus* sp., *Volvox* sp., anisopteran and zygopteran nymphs, and dissolved oxygen levels were suppressed in the presence of bluegill. *Diaptomus* sp., *Conochiloides* sp., *Cyclotella* sp., *Navicula* sp., *Oocystis* sp., *Anabaena* sp., *Ceratium* sp., algal fluorescence, turbidity, 5- to 12.7-μm particles, and total phosphorus and total nitrogen were enhanced in the presence of bluegill. *Daphnia pulicaria* was enhanced and *Cyclotella* sp. and *Oocystis* sp. were suppressed in the presence of largemouth bass. Although the effects of the two fish were not independent, as indicated by significant bluegill × largemouth bass interactions for some plankton taxa, we found little evidence of bluegill impacts being reversed by largemouth bass. While total bluegill biomass was reduced and bluegill biomass distributions were shifted toward larger individuals, bluegill remained abundant in the presence of largemouth bass.

Nous avons examiné les répercussions qu'ont sur la communauté les crapets arlequins (*Lepomis macrochirus*) et les achigans à grande bouche (*Micropterus salmoides*) au cours d'une étude expérimentale réalisée pendant l'été dans un étang suivant un plan factoriel avec quatre combinaisons de traitement (sans poisson, crapet arlequin, achigan à grande bouche et crapet arlequin avec achigan à grande bouche). En présence de crapets arlequins, les concentrations d'oxygène dissous et le nombre de nymphes d'anisoptères et de zygoptères, de *Ceriodaphnia reticulata*, de *Daphnia pulicaria*, de *Chaoborus* sp. et de *Volvox* sp. ont diminué. Par contre, en leur présence, il y a eu augmentation du nombre de *Diaptomus* sp., de *Conochiloides* sp., de *Cyclotella* sp., de *Navicula* sp., d'*Oocystis* sp., d'*Anabaena* sp., de *Ceratium* sp., augmentation de la fluorescence des algues, de la turbidité, des particules d'un diamètre variant de 5 à 12,7 μm ainsi que du phosphore et de l'azote totaux. En présence d'achigans à grande bouche, le nombre de *D. pulicaria* a augmenté tandis que celui de *Cyclotella* sp. et d'*Oocystis* sp. a diminué. Bien que les effets des deux espèces de poisson n'étaient pas indépendants, tel qu'indiqué par les interactions importantes entre le crapet arlequin et l'achigan à grande bouche relativement à certains taxons de plancton, nous avons trouvé peu d'indications qui laissent croire que les répercussions des crapets arlequins soient renversées par les achigans à grande bouche. Bien que la biomasse totale de crapets arlequins ait diminué et que la répartition de leur biomasse se soit déplacée vers des individus plus gros, les crapets arlequins sont restés nombreux en présence d'achigans à grande bouche.

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Most experimental studies examining community impacts of fish have focused on planktivorous fish which are internal regulators of plankton community structure of lakes (Zaret 1980; Hurlbert and Mulla 1981). While piscivorous fish are top level consumers in most lakes and may affect plankton communities through predation on planktivorous fish, few workers have examined whether planktivore impacts are influenced by piscivory (Zaret and Paine 1973; Benndorf et al. 1984; Shapiro and Wright 1984; Spencer and King 1984). These studies show that the reduction of planktivore populations by piscivores results in a reversal or decline in intensity of planktivore effects. In this paper, we present results from an experimental pond study examining summer plankton community responses to planktivorous bluegill (*Lepomis macrochirus*) in the presence and absence of piscivorous largemouth bass (*Micropterus salmoides*). We show that suppression of large zooplankton and enhancement of phytoplankton by bluegill are not significantly reversed in the presence of largemouth bass.

Materials and Methods

The study was conducted at the University of Kansas Nelson Environmental Study Area (NESA) from 5 June to

30 September 1983, in two mud-bottomed ponds, each divided by concrete partitions into four 0.006-ha, 61-m^3 quadrants (approximately 6.0 × 7.0 × 1.4 m). A 2 × 2 factorial design (presence and absence of bluegill × presence and absence of largemouth bass) resulted in four treatment combinations: (1) fishless, (2) bluegill, (3) largemouth bass, and (4) bluegill with largemouth bass. Each treatment combination was replicated twice and assigned to quadrants using a randomized block design.

Before the experiment, macrophytes (primarily *Typha* sp. and *Salix* sp.) were removed from the ponds. To provide similar initial sediment and water chemistry in the ponds, each was alternately filled with well water, mixed by wading to suspend sediments, and then partially emptied into the other pond via underground plumbing. Both ponds were then drained and a 3.7 × 7.6 m plastic sheet placed over the central portion (approximately 50%) of each quadrant bottom to prevent excessive macrophytic growth. The uncovered areas of each quadrant were recolonized by macrophytes during the study. Ponds were filled with water from a fishless reservoir on 4–5 June (17:00–09:00). Water temperature was initially 20°C and increased to 29°C by August. The ponds did not stratify.

Fish were collected from Potter's Lake and West Campus Pond on the University of Kansas campus, a pond at NESA, and two ponds located approximately 24 km southwest of Lawrence. Fish were collected by either shoreline-seining or hook and line and transferred to NESA holding ponds for 2 wk prior to stocking. Bluegills (135–144 individuals/quadrant) were stocked on 23 June and largemouth bass (3 individuals/quadrant) on 24 June at 280 and 112 kg/ha, respectively, which are standing crops typically found in Kansas ponds (D. Gablehouse, Kansas Fish and Game Commission, pers. comm.). We apportioned fish biomass into three size classes of bluegill (small, intermediate, and large) and two size classes of largemouth bass (small and large) to mimic mean biomass frequency distributions which we calculated for 26 balanced bluegill/largemouth bass communities presented in Swingle (1950) (Fig. 1). Swingle characterized balanced communities as having (1) ratios of total forage fish biomass to total piscivorous fish biomass (F/C) ranging from 1.4 to 10.0, (2) ratios of small forage fish biomass to total piscivorous fish biomass (Y/C) ranging from 0.02 to 5.0, (3) more than 40% of the total fish biomass in the form of harvestable fish (A_T value), and (4) at least 18%, but preferably more than 35%, of the total bluegill biomass in the form of harvestable bluegills (A_F value). He defined small bluegills as those with body depths less than the mean piscivore mouth width. Intermediate bluegills have body depths greater than the mean piscivore mouth width, but are too small for angler harvest. Large bluegills also have body depths greater than the mean piscivore mouth width, but are large enough for angler harvest. Large and small largemouth bass are those which can and cannot be harvested by anglers. In our study the size ranges of small, intermediate, and large bluegills were 30–89, 90–127, and 128–203 mm total length (TL) and of small and large largemouth bass were 178–234 and 235–320 mm TL, respectively. Our ponds met Swingle's criteria for balance at the beginning and end of the experiment as shown by F/C values of 2.87 ± 0.13 and 2.65 ± 0.17, Y/C values of 1.04 ± 0.04 and 0.69 ± 0.10, A_T values of 0.66 and 0.69 ± 0.02, and A_F values of 0.58 ± 0.01 and 0.59 ± 0.05, respectively. Although bluegills spawned in all quadrants and largemouth bass did not, the fish communities remained balanced at pond drainage due to largemouth bass growth.

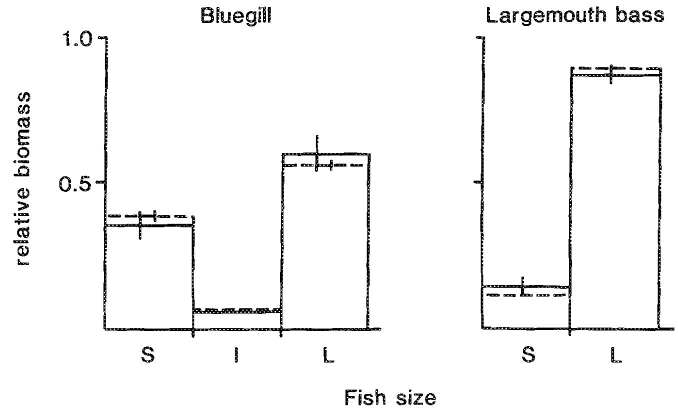

FIG. 1. Comparison of biomass frequency distributions of bluegill and largemouth bass stocked in pond quadrants (solid line) with biomass distributions in balanced bluegill/largemouth bass pond communities (Swingle 1950) (broken line). S = small, I = intermediate, and L = large. Vertical bars represent ± 1 SE.

On 30 September, fish and bullfrog tadpoles (*Rana catesbieana*) were recovered by rotenone poisoning. After rotenoning, ponds were checked for 1 wk to ensure recovery of all fish and tadpoles. One largemouth bass was not recovered and another was recovered from a bluegill quadrant. Because largemouth bass were last observed to be in proper quadrants on 5 August, we have limited our analyses to the period 5 June – 5 August.

Beginning on 5 June, zooplankton were sampled every 10 d between 22:00 and 02:00. Two samples were taken from each quadrant by vertical tows of a 63-μm-mesh conical plankton net (29.5-cm diameter) and preserved in 5% sucrose–formalin. Zooplankters were counted from 1-mL subsamples until the standard deviation of each count fell within 10% of the mean for each taxon. Zooplankters were identified according to Pennak (1953), Edmondson (1959), and Ruttner-Kolisko (1974). Phytoplankton were sampled between 08:00 and 10:00 on three days prior to fish stocking (5, 13, 19 June) and on four days after stocking (25 June, 5, 15, 27 July). Nannoplankton were collected using a deNoyelles' integrated phytoplankton sampler (deNoyelles and O'Brien 1978) which quantitatively samples the water column. The contents of the sampler were discharged into a plastic container, mixed, and subsampled (two 125-mL aliquots). Each quadrant was sampled twice, resulting in four 125-mL subsamples. Two subsamples were preserved in 1% Lugol's solution and two were used to determine algal fluorescence (Turner model 10 Rackmount Fluorometer), turbidity (HACH Turbidimeter), and particle densities (model ZB Coulter Counter, 100-μm aperature tube).

After thorough mixing, volumes (5, 10, or 25 mL) of the preserved subsamples were placed into sedimentation chambers using a large-orifice pipette and allowed to settle overnight (Sournia 1978). The volume settled was selected to provide a density ≥2 algal cells per field. After settling, the supernatant was removed and a coverglass placed over the bottom chamber. Twenty-five fields were counted along 10 transects using a Wild M40 phase contrast inverted microscope. The chamber was then turned 90° and an additional 25 fields counted. Net phytoplankton were counted in a similar manner but using 1-mL subsamples from the zooplankton samples. Identifications were made according to Prescott (1962, 1970) and Whitford and Schumacher (1973).

Alkalinity (potentiometric titration, APHA 1980), pH

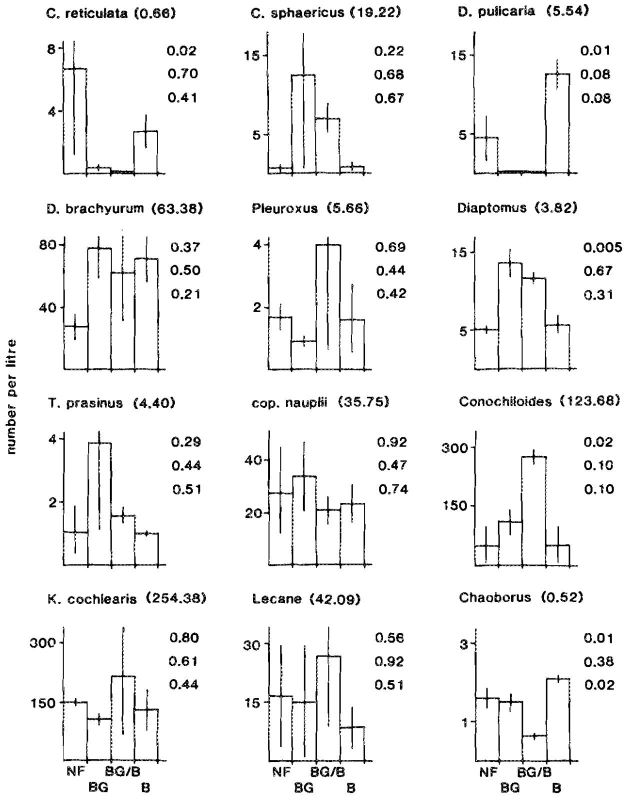

FIG. 2. Mean number of zooplankters per litre after fish stocking (24 June – 5 August) in fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Probability values for bluegill (upper) and largemouth bass (middle) main effects and interactions (lower) are given to the right of each histogram. Vertical bars represent ± 1 SE. $\sqrt{MS_{error}}$ shown in parentheses.

(Sargent–Welch pH meter), and dissolved oxygen (YSI meter and Winkler Titration, APHA 1980) were measured on each sampling date. On 5, 9, and 10 June, 11, 13, and 17 July, and 30 September, additional water samples were frozen for analysis of total phosphorus (TP) and total nitrogen (TN). Two 25-mL samples were analyzed from each quadrant on each sampling date. Samples for TP were digested with potassium persulfate (Menzel and Corwin 1965) and analyzed by a modification of the ascorbic acid method (APHA 1980) in which 4 mL of color reagent was added to 25-mL samples and read at 665 nm (D. Wright, Limnological Research Center, University of Minnesota, Minneapolis, MN, pers. comm.). Samples for TN were digested with alkaline potassium persulfate (D'Elia et al. 1977) and analyzed using the UV absorption method (APHA 1980).

Macroinvertebrates (primarily anisopteran and zygopteran nymphs; Order Odonata) were sampled on 14, 22, and 28 July and 5 August between 22:00 and 02:00 with a 63-μm-mesh conical plankton net (19.5-cm diameter). The net, attached to a pole, was pushed through the macrophytic vegetation along the length of the concrete partitions in each quadrant 0.75 m below the water surface. Samples were preserved in 5% sucrose–formalin, and all odonate nymphs were counted and identified using Pennak (1953).

Sampling of ponds produced time series data which were analyzed by a split-plot ANOVA with repeated measures on one factor. This ANOVA accounts for the autocorrelation of

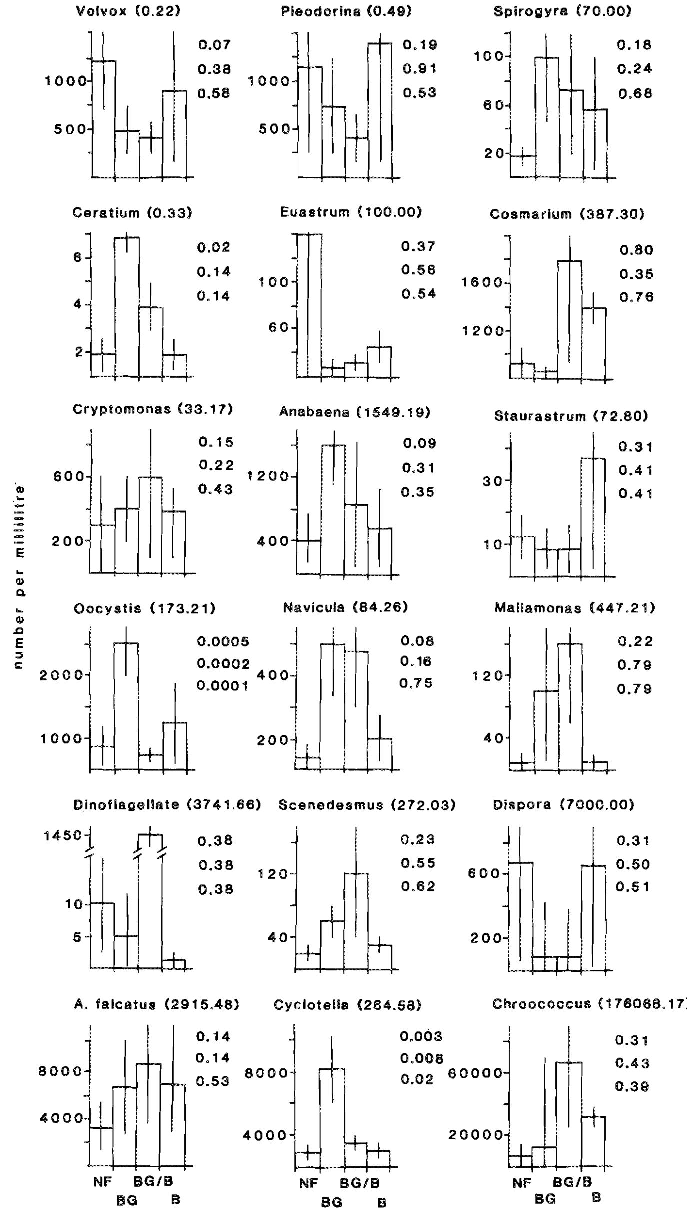

FIG. 3. Mean number of phytoplankton per millilitre after fish stocking (24 June – 27 July) in fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Probability values for bluegill (upper) and largemouth bass (middle) main effects and interactions (lower) are given to the right of each histogram. Vertical bars represent ± 1 SE. $\sqrt{MS_{error}}$ shown in parentheses.

pond samples through time (Winer 1971; Gill 1978). The analysis generates three effects terms: main effects, interactions, and simple effects. Main effects allow independent assessments of the impact of each factor (bluegill and largemouth bass), interactions allow assessment of the interdependence among factors, and simple effects allow for a further examination of interactions through direct comparison of treatment combinations. To evaluate variability between quadrants prior to fish introduction, quadrants were paired as if fish were present.

A past study at NESA involved fertilization of one of the experimental ponds and may have contributed to variation between treatment replicates. A preliminary test on the model was performed at $\alpha = 0.25$ to remove confounding pond

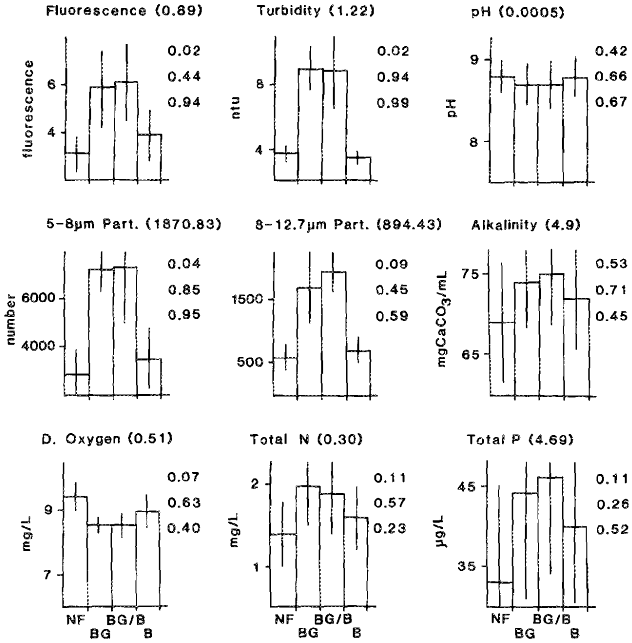

FIG. 4. Mean levels of algal fluorescence, turbidity, electronically counted particles, and water chemistry parameters after fish stocking (24 June − 27 July) in fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Probability values for bluegill (upper) and largemouth bass (middle) main effects and interactions (lower) are given to the right of each histogram. Vertical bars represent ± 1 SE. $\sqrt{MS_{error}}$ shown in parentheses.

(block) effects (Sokal and Rohlf 1969; Winer 1971). All significant pond effects ($\alpha \leq 0.25$) were dropped and the remaining sums of squares and degrees of freedom pooled to calculate a residual MS error term (Sokal and Rohlf 1969). Alpha was set at 0.25 to reduce the chance of committing a type II error (β) (Winer 1971). The experimental design and twofold replication resulted in low sensitivity for determining bluegill × largemouth bass interactions. The experiment was capable of detecting bluegill × largemouth bass interactions $\geq 2.6 \sqrt{MS_{error}}$ at $\alpha = 0.10$, with $\beta \leq 0.10$.

Results

Ceriodaphnia reticulata, *Daphnia pulicaria*, *Chaoborus* sp., *Volvox* sp., and zygopteran and anisopteran nymphs were less abundant in the presence of bluegill (Fig. 2, 3, and 5). *Diaptomus* sp., *Conochiloides* sp., *Cyclotella* sp., *Navicula* sp., *Oocystis* sp., *Anabaena* sp., *Ceratium* sp., algal fluorescence, turbidity, and 5- to 8-μm and 8- to 12.7-μm particles were higher in quadrants with bluegill (Fig. 2, 3, and 4). TP and TN were higher and dissolved oxygen was lower in treatments with bluegill (Fig. 4). Largemouth bass had no effects on odonate nymphs or water chemistry but were associated with a higher abundance of *D. pulicaria* and lower abundances of *Cyclotella* sp. and *Oocystis* sp. (Fig. 2 and 3). Significant bluegill × largemouth bass interactions were detected for *Chaoborus* sp., *D. pulicaria*, *Conochiloides* sp., *Cyclotella* sp., and *Oocystis* sp. (Fig. 2 and 3). Analysis of these interactions by simple effects indicates that *Chaoborus* sp., *Cyclotella* sp., and *Oocystis* sp. were significantly less abundant (P = 0.02, 0.004, and 0.01, respectively) in bluegill/largemouth bass

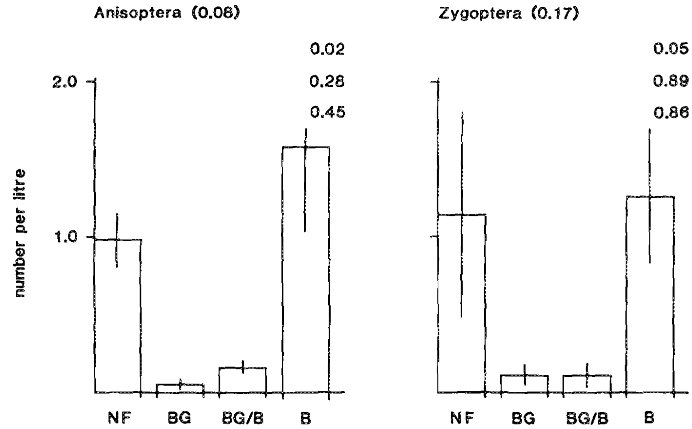

FIG. 5. Mean number of anisopteran and zygopteran (Order Odonata) nymphs per litre after fish stocking (24 June − 5 August) in fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Probability values for bluegill (upper) and largemouth bass (middle) main effects and interactions (lower) are given. Vertical bars represent ± 1 SE. $\sqrt{MS_{error}}$ shown in parentheses.

TABLE 1. Bluegill biomass stocked and recovered in replicates a and b of bluegill (BG) and bluegill/largemouth bass (BG/B) treatment combinations.

		Biomass (g)	
		Stocked	Recovered
BG	a	1812.7	1934.0
	b	1502.4	2152.3
BG/B	a	1880.2	1865.6
	b	1783.0	1655.2

quadrants relative to bluegill quadrants. *Conochiloides* sp. were higher in abundance in bluegill/largemouth bass quadrants relative to bluegill quadrants (P = 0.04). In bluegill/largemouth bass quadrants, *D. pulicaria* decreased in abundance relative to bass quadrants (P = 0.009), but were similar (P = 0.86) to those in bluegill quadrants. None of these main or interaction effects were detected prior to fish introduction.

Recovery data of fish on 30 September showed that bluegill biomass in bluegill/largemouth bass quadrants was approximately 15% lower relative to bluegill quadrants (Table 1). While bluegill biomass distributions were shifted toward the larger size class (Fig. 6), 33 and 41% of the bluegill biomass was small enough to be consumed by the largest bass in each bluegill/largemouth bass quadrant. Tadpole biomass was highest in quadrants with only bluegill and lower in quadrants containing largemouth bass (Fig. 7).

Discussion

Bluegill typically suppress populations of large-bodied zooplankters and odonates, but enhance populations of phytoplankton and small-bodied and highly evasive zooplankton and nutrient levels (Hall et al. 1970; Werner and Hall 1976; Bartell 1982; Lynch and Shapiro 1981; Crowder and Cooper 1982; Morin 1984). Phytoplankton increases have been attributed to changes in zooplankton community structure or alteration of nutrient cycles (Lamarra 1975; Hurlbert and Mulla 1981).

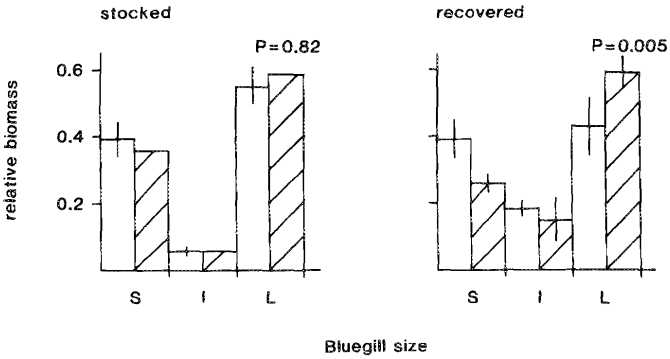

FIG. 6. Bluegill biomass distributions stocked and recovered in bluegill (open bars) and bluegill/largemouth bass (hatched bars) treatment combinations and the results of a chi-squared analysis. S = small, I = intermediate, and L = large. Vertical bars represent ± 1 SE.

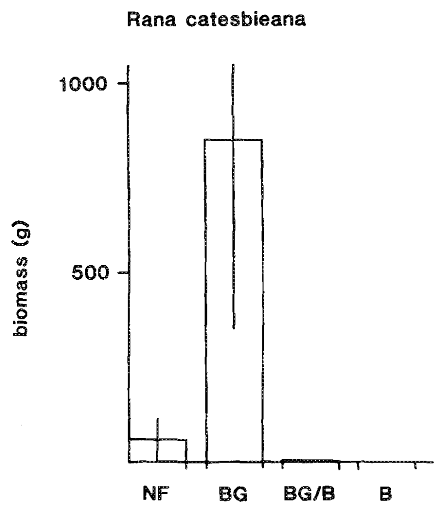

FIG. 7. Mean tadpole (*Rana catesbieana*) biomass recovered from fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Vertical bars represent the range between replicates.

Because bluegill suppressed large herbivorous zooplankton and increased phosphorus and nitrogen levels, we cannot discriminate between these two alternative mechanisms. Although tadpoles are algal grazers and can suppress phytoplankton populations (Dickman 1968; Seale 1980), tadpole effects on phytoplankton were not apparent. Bluegill enhancement of phytoplankton was similar in both the presence and absence of tadpoles.

While significant interactions between largemouth bass and bluegill indicate that some of the impacts of the two fish were not independent, we found little evidence of bluegill impacts being reversed by largemouth bass. Piscivores can affect planktivores either by causing a change in planktivore feeding habits or by reducing the planktivore populations. Werner et al. (1983) found that the presence of largemouth bass was correlated with a delay in shift of feeding habitat from the littoral to the pelagic zone by young bluegill. We did not examine bluegill habitat choice. However, the small size of the ponds may not have permitted a habitat shift by bluegill.

Studies showing a reduction of planktivore biomass by piscivores (Zaret and Paine 1973; Benndorf et al. 1984; Spencer and King 1984) involved minnow-like planktivores which are highly vulnerable to piscivory because of their small size. Bluegill are deep bodied and can grow to a size not available to largemouth bass, providing adult bluegill a size refugium from largemouth bass predation (Lawrence 1957; Werner et al. 1983). However, Shapiro and Wright (1984) showed that piscivores can reverse bluegill impacts on plankton communities and nutrients if fish are stocked in a high piscivore to planktivore ratio.

Although the low replication, short duration of the study, and failure of largemouth bass to reproduce limited our ability to detect largemouth bass effects on the plankton community response to bluegill, our study suggests that bluegill effects may not be reversed by largemouth bass when the fish populations occur at natural standing crops. Because they have coevolved with largemouth bass and have behavioral and physical characteristics which reduce their vulnerability to piscivory (Howick and O'Brien 1983), bluegills are typically abundant in lakes containing largemouth bass (Cooper et al. 1971; Carlander 1977).

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