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Context-dependent effects of bluegill in experimental mesocosm communities

Received: 3 November 1998 / Accepted: 24 September 1999

Abstract Most knowledge of direct and indirect effects of zooplanktivorous fish has come from studies in which a treatment with a zooplanktivore is compared to a fishless control. However, effects of a zooplanktivore may be different in the presence of other fish species because the other fish have direct and indirect effects that may alter the effects of the zooplanktivore in question. To test this hypothesis, we conducted a tank mesocosm experiment of 2×2 factorial design in which the presence and absence of bluegill (*Lepomis macrochirus*) were cross-classified with the presence and absence of a fish assemblage composed of western mosquitofish (*Gambusia affinis*) and common carp (*Cyprinus carpio*). The presence of bluegill decreased *Daphnia*, *Ceriodaphnia*, cyclopoid copepodids, calanoid copepodids, copepod nauplii, amphipods, gastropods, and notonectids. *Daphnia*, *Ceriodaphnia*, cyclopoid copepodids, copepod nauplii, gastropods, notonectids, *Najas*, and *Chara* were decreased and herbivorous rotifers, turbidity, chlorophyll *a*, total nitrogen and total phosphorus were increased in the presence of the fish assemblage. Significant bluegill×fish assemblage interaction effects were detected for *Daphnia*, *Ceriodaphnia*, cyclopoid copepodids, copepod nauplii, gastropods, and notonectids. Analysis of simple effects for these response variables revealed that all significant bluegill effects in the absence of the fish assemblage were not significant in the presence of the fish assemblage. Our results indicate that the effects of bluegill may be context dependent, or dependent upon the presence of other trophically similar fish species.

Key words Bluegill · Zooplanktivore · Context dependence · Keystone species · Microcosms

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Introduction

Zooplanktivorous fish have direct and indirect effects which regulate zooplankton and phytoplankton community structure (Lazzaro 1987; Northcote 1988). Visually foraging zooplanktivores can directly suppress larger zooplankton species and indirectly enhance smaller zooplankton species. Zooplanktivorous fish can also indirectly enhance phytoplankton through the direct suppression of large herbivorous zooplankton and modification of nutrient cycling (Vanni 1997a, 1997b).

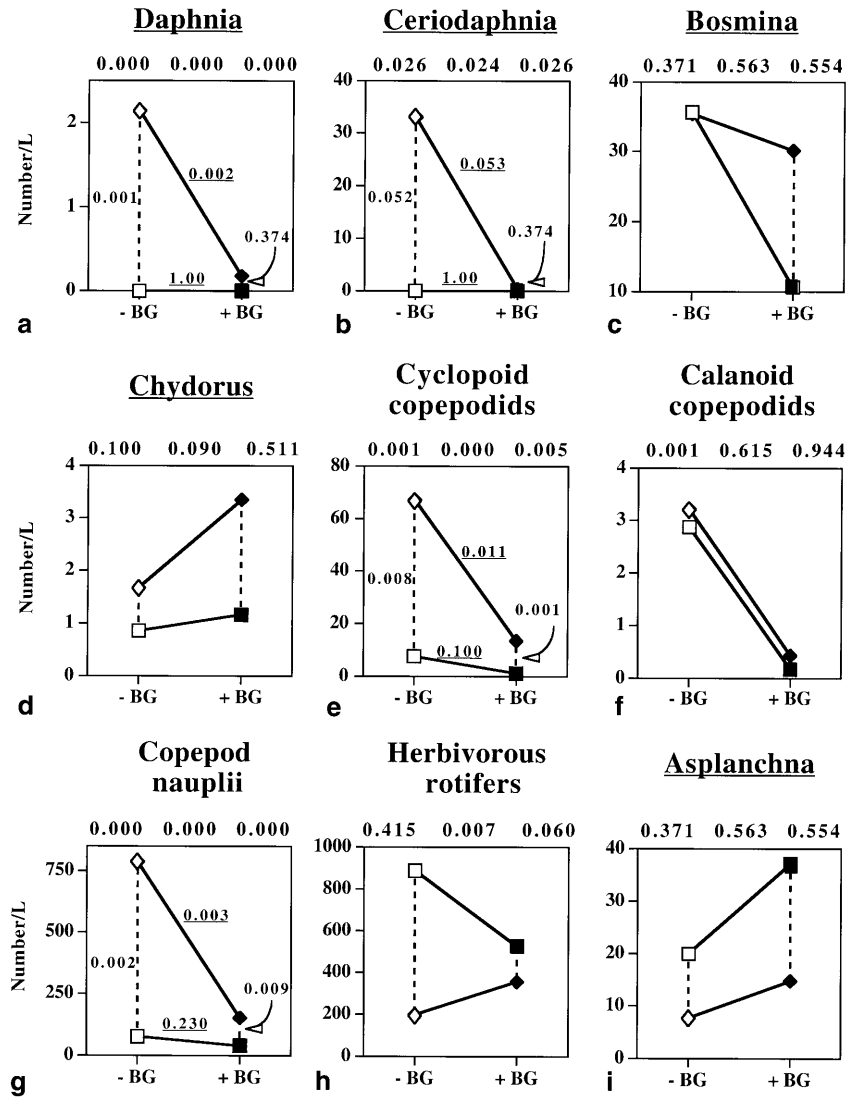
Most knowledge about the impacts of zooplanktivorous fish on zooplankton and phytoplankton has come from experiments whose design comprises comparison of a fishless control treatment with a treatment including a single species of zooplanktivorous fish (Lazzaro 1987; Northcote 1988). Although this type of experimental design allows ecologists to examine the most dramatic effects of a zooplanktivore, the results may not apply to systems containing other fish species which may also have direct and indirect effects that can alter the effects of the zooplanktivore in question (Magnan 1988). For example, Brooks and Dodson (1965) found that the introduction of the zooplanktivorous blueback herring (*Alosa aestivalis*) into a fishless lake caused a dramatic shift in the size distribution of the zooplankton community. However, the sizes of zooplankton did not significantly change when blueback herring were introduced into a reservoir that contained several other species of zooplanktivorous fish (Guest and Drenner 1991).

To explore how the effects of a zooplanktivore may be affected by the presence of other fish species, we conducted a mesocosm experiment in which the effects of bluegill (*Lepomis macrochirus*) were studied in the presence and absence of a fish assemblage consisting of a combination of two fish species [western mosquitofish (*Gambusia affinis*) and common carp (*Cyprinus carpio*)]. We selected bluegill because it is widely distributed in North America (Page and Burr 1991) and thought to act as a keystone species (Menge et al. 1994), even

Table 1 Studies examining the effects of bluegill on zooplankton, phytoplankton, and macroinvertebrates (where applicable) from a literature search of the following eight journals (volumes and years indicated): *Archiv für Hydrobiologie* (vol. 102–137, 1984–1996), *Canadian Journal of Fisheries and Aquatic Sciences* (vol. 37–53, 1980–1996), *Ecology* (vol. 61–77, 1980–1996), *Freshwater Biology* (vol. 10–36, 1980–1996), *Hydrobiologia* (vol. 68–339, 1980–1996), *Limnology and Oceanography* (vol. 25–41, 1980–1996), *Oecologia* (vol. 44–108, 1980–1996), and *Oikos* (vol. 44–77, 1985–1996). Studies referenced by papers found in the search are also included in the table: Hall et al. (1970), Lynch (1979), Lynch (1987b), and Vanni (1987b) (N/A not applicable)

	Hall et al. 1970	Lynch 1979	Lynch and Shapiro 1981	Hambright et al. 1986	Vanni 1986	Vanni 1987a, 1987b	Drenner et al. 1990	Starling and Rocha 1990	Turner and Mittelbach 1990	Leibold 1991	Lazzaro et al. 1992	Turner and Mittelbach 1992
Experimental system	Small ponds	Enclosure bags	Enclosure bags	Small ponds	Enclosure bags	Enclosure bags	Mesocosm tanks	Enclosure bags	Partitioned ponds	Enclosure bags	Mesocosm tanks	Enclosure bags
Experimental design	Factorial design	Five levels of bluegill	Experiment A: five levels of bluegill biomass; experiment B: factorial design (2 bluegill × 3 nutrient)	Factorial design (2 bluegill × largemouth bass)	Experiment A and B: presence and absence of bluegill	Experiment A and B: factorial design (2 bluegill × 3 nutrient)	Factorial design (2 bluegill × 3 nutrient)	Presence and absence of bluegill	Bluegill in presence and absence of largemouth bass	Factorial design (2 bluegill × zooplankton assemblages)	Five levels of bluegill biomass	Presence and absence of bluegill × presence of <i>Daphnia</i> or <i>Ceriodaphnia</i>
Other fish species present	None	None	None	Largemouth bass	None	None	None	None	Largemouth bass	None	None	None
Effects on zooplankton	Decreased large taxa, increased small taxa	Decreased large taxa, increased small taxa	Experiment A and B: decreased large taxa, increased small taxa	Decreased <i>Daphnia</i> and <i>Ceriodaphnia</i>	Experiment A: decreased cladoceran body size; experiment B: decreased large taxa, increased small taxa	Experiment A and B: decreased large taxa, increased small taxa	Decreased cladocerans and cyclopoid copepods, increased rotifers	Increased rotifers	Decreased <i>Daphnia</i>	Decreased <i>Daphnia</i>	Decreased cladocerans and copepods, increased rotifers	Decreased cladocerans, increased small taxa
Effects on phytoplankton	No effect	Increased algal density	Experiment A and B: increased algal biomass	Increased algal fluorescence	Experiment A and B: increased some algal taxa	Experiment A: increased algal biovolume; experiment B: increased some algal taxa	Increased some algal taxa	Increased some algal taxa	No effect	Increased algal fluorescence	Increased phytoplankton biomass	Increased algal biomass
Effects on macroinvertebrates	Decreased some taxa	N/A	N/A	Decreased odonates	N/A	N/A	Decreased chironomid tubes	N/A	N/A	N/A	Decreased chironomid tubes	N/A

Fig. 1a–i Factorial graphs of the effects of bluegill and the fish assemblage on zooplankton. Points within each panel represent the mean of three replicates of each treatment combination for the entire experimental period [*open diamond* bluegill absent (–BG), fish assemblage absent; *closed diamond* bluegill present (+BG), fish assemblage absent; *open square* bluegill absent, fish assemblage present; *closed square* bluegill present, fish assemblage present]. Numbers at the top of each panel are *P*-values for (from left to right) the main effects of bluegill and the fish assemblage and the bluegill×fish assemblage interaction effect. For response variables having significant interaction effects, *P*-values for simple effects are included on the panels. *P*-values for the simple effects of bluegill (*underlined*) in the absence and presence of the fish assemblage are represented by numbers next to *solid lines*. *P*-values for the simple effects of the fish assemblage in the absence and presence of bluegill are represented by numbers next to *dashed lines*



though the effects of bluegill on plankton have been almost exclusively studied in the absence of other fish species (Table 1).

Materials and methods

The experiment was conducted in 12 fiberglass mesocosm tanks (0.6 m² surface area, 500 l) located at the Eagle Mountain Fish Hatchery, Fort Worth, Texas. The experiment consisted of a 2×2 factorial design in which the presence and absence of bluegill were cross-classified with the presence and absence of a fish assemblage composed of western mosquitofish and common carp. Mosquitofish and common carp were selected as members of the fish assemblage because they represent two fish consumer types found in lake communities. Mosquitofish is a carnivore that consumes zooplankton and benthic invertebrates (Hurlbert et al. 1972; Hurlbert and Mulla 1981; Drenner et al. 1989; Lancaster and Drenner 1990) and carp is a benthivore (Richardson et al. 1990). Both species are distributed throughout the United States (Page and Burr 1991) and commonly co-occur with bluegill (Miranda 1983).

On 18 April 1997, sediment was collected from below the water line of eight ponds located at the hatchery, combined, and an aliquot of this mixture was added to the bottom of each mesocosm

to create a 15-cm-deep layer. The mesocosms were filled with water piped from the epilimnion of Eagle Mountain Lake, a eutrophic reservoir adjacent to the hatchery. On 25 April, zooplankton were collected from each of the eight ponds with one vertical tow of a 12-cm-diameter 80- μ m Wisconsin plankton net, mixed in a bucket, and 1 l of this mixture was added to each mesocosm.

Treatments were randomly assigned to mesocosms and fish were stocked on 2 May. Each of the four treatment combinations was replicated three times. The bluegill treatment was composed of three bluegill [mean total length (TL)=4.7 cm, range=3.8–5.9 cm] at a mean total biomass (wet weight) of 2.3 g/tank (range=2.1–2.5 g/tank). The fish assemblage treatment consisted of two mosquitofish (mean TL=4.4 cm, range=3.7–4.9 cm) and one common carp (mean TL=12.4 cm, range=11.9–13.2 cm) at mean total biomasses (wet weight) of 2.2 g/tank (range=2.0–2.5 g/tank) and 11.9 g/tank (range=9.5–15.3 g/tank), respectively. To prevent bird predation and fish from jumping out, mesocosms were covered with plastic netting with 1.5 cm mesh. Because dead fish can alter nutrient concentration in mesocosm experiments (Threlkeld 1988), mesocosms were monitored every 2 days for dead fish. During the experiment, one carp died, was removed and replaced with a carp of approximately the same size and weight.

The experiment was conducted for 28 days after fish had been stocked. Samples for turbidity, chlorophyll *a*, total phosphorus (TP), total nitrogen (TN), and zooplankton were collected every

Fig. 2a–d Factorial graphs of the effects of bluegill and the fish assemblage on macroinvertebrates. Points within each panel represent the mean of three replicates of each treatment combination for the entire experimental period. Symbols and significance values as in Fig. 1)

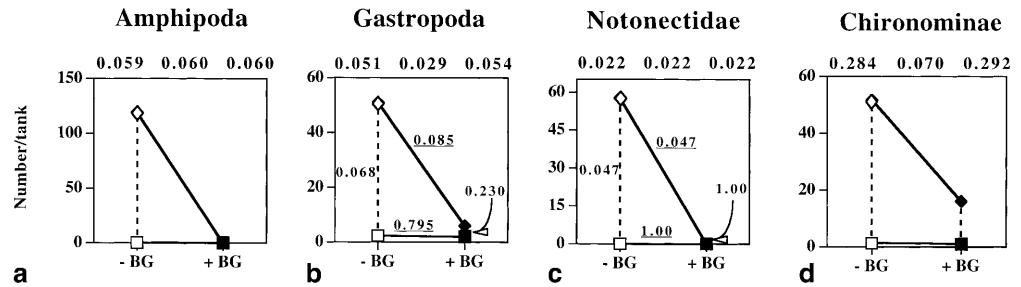
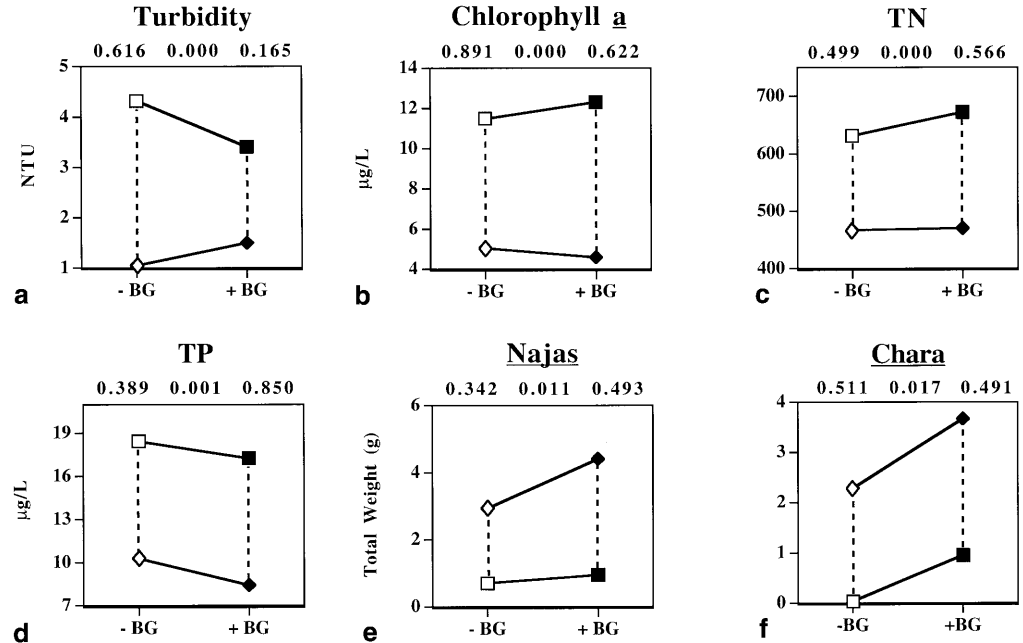


Fig. 3a–f Factorial graphs of the effects of bluegill and the fish assemblage on turbidity, chlorophyll *a*, nutrients (*TN* total nitrogen, *TP* total phosphorus) and macrophytes. Symbols as in Fig. 1. Numbers at the top of each panel are (from left to right) *P*-values for the main effects of bluegill and the fish assemblage and the bluegill×fish assemblage interaction effect. No simple effects are presented because no significant interaction effects were detected



7 days for four sampling dates. To collect samples for turbidity, chlorophyll *a*, TP, and TN, a 2-l plastic pitcher was inverted under water in each tank. Turbidity was measured on a Hach 2100A turbidimeter. For chlorophyll *a* analyses, water was filtered through 0.45-µm Millipore HAWP membrane filters. The filters were wrapped in aluminum foil and frozen. Chlorophyll *a* was extracted with a 2:1 chloroform:methanol solution at room temperature for a minimum of 8 h in the dark and read at 665 nm (Wood 1985). Samples for TP and TN were stored at -10°C in plastic Nalgene bottles. TP was determined by digestion with potassium persulfate (Menzel and Corwin 1965) and analyzed with the malachite green method (Van Veldhoven and Mannaerts 1987) with absorbance measured at 610 nm. TN was determined by digestion with alkaline potassium persulfate (D'Elia et al. 1977) with UV absorbance measured at 220 nm (American Public Health Association 1985). Zooplankton were collected with one vertical tow per mesocosm of a 12-cm-diameter 80-µm Wisconsin plankton net, preserved in 10% sugar-formalin (Haney and Hall 1973) and counted with a Wild dissecting stereomicroscope at ×25 magnification. Zooplankton densities were not corrected for net efficiency.

Macroinvertebrates were sampled at the end of the experiment by siphoning water from mesocosms with a 1.6-cm-diameter hose through an 80-µm mesh net. Organisms were preserved with 10% sugar-formalin, sorted into taxonomic groups and the total number of each taxon per mesocosm was determined. When the water level of a mesocosm was 10 cm above the bottom sediments, macrophytes were removed by cutting stems at the sediment surface. Macrophytes were sorted by species and dried in an incubator at 37°C for 2 weeks and the total dry mass of each species was determined. Fish were removed with dip nets and weighed.

Statistical analysis was performed with two-way ANOVA for cross-classified factors, allowing us to examine main and interaction effects. Main effects are the independent impact of each factor (bluegill or fish assemblage) and interaction effects are the amount of measured variation in the response variables due to the interdependence between bluegill and the fish assemblage. If significant bluegill×fish assemblage interaction effects were detected, we performed an analysis of simple effects. Analysis of simple effects allowed us to determine if the effects of a treatment factor were different in the presence and absence of the other factor. Simple effects of bluegill and the fish assemblage were obtained with a one-way ANOVA. Statistical significance for all analyses was inferred at $P \leq 0.05$. Because we did not wish to address possible seasonal effects in the 29-day experiment, statistical analyses were performed on the mean value for each response variable across all sampling dates. Statistical analyses were performed on SYSTAT version 5.2.1 (Wilkinson et al. 1992).

Results

The abundances of *Daphnia*, *Ceriodaphnia*, cyclopoid copepodids, calanoid copepodids, copepod nauplii (Fig. 1), amphipods, gastropods, and notonectids (Fig. 2) were decreased in the presence of bluegill. The presence of the fish assemblage decreased abundances of *Daphnia*, *Ceriodaphnia*, cyclopoid copepodids, and copepod nauplii and increased herbivorous rotifers (Fig. 1). The presence of the

fish assemblage also decreased gastropods and notonectids (Fig. 2). Turbidity, chlorophyll *a*, TN, and TP were increased and the total dry masses of *Najas* and *Chara* were decreased in the presence of the fish assemblage, but not significantly affected by the presence of bluegill (Fig. 3).

Significant bluegill×fish assemblage interaction effects were detected for *Daphnia*, *Ceriodaphnia*, cyclopoid copepodids, copepod nauplii (Fig. 1), gastropods, and notonectids (Fig. 2), indicating interdependence between the effects of bluegill and the fish assemblage for these response variables. We used analysis of simple effects on these response variables to examine how the effects of bluegill differed in the presence and absence of the fish assemblage and how the effects of the fish assemblage differed in the presence and absence of bluegill. Bluegill significantly decreased densities of *Daphnia* ($P=0.002$), *Ceriodaphnia* ($P=0.053$), cyclopoid copepodids ($P=0.011$), copepod nauplii ($P=0.003$) (Fig. 1) and notonectids ($P=0.047$) (Fig. 2) in the absence of the fish assemblage, but all of these effects were not significant in the presence of the fish assemblage. The presence of the fish assemblage decreased densities of *Daphnia* ($P=0.001$) and *Ceriodaphnia* ($P=0.052$) (Fig. 1) and notonectids ($P=0.047$) (Fig. 2) only in the absence of bluegill. The presence of the fish assemblage significantly decreased cyclopoid copepodids and copepod nauplii (Fig. 1) in both the presence and absence of bluegill.

Discussion

Previous studies examining the effects of bluegill in the absence of other fish species found that bluegill reduced densities of large zooplankton taxa and increased smaller zooplankton taxa, turbidity, nutrients, and phytoplankton, but the effects varied between studies (Table 1). Bluegill also altered the size structure and species composition of macroinvertebrate communities (Table 1). In our study, in the absence of the fish assemblage, bluegill had similar effects and appeared to function as a dominant controlling agent of invertebrate community structure by reducing densities of *Daphnia*, *Ceriodaphnia*, cyclopoid copepodids, calanoid copepodids, copepod nauplii (Fig. 1), amphipods, gastropods, and notonectids (Fig. 2).

The effects of bluegill were not independent of the presence of the fish assemblage. Densities of *Daphnia*, *Ceriodaphnia*, cyclopoid copepodids, copepod nauplii (Fig. 1), gastropods and notonectids (Fig. 2) exhibited significant bluegill×fish assemblage interaction effects. The analysis of simple effects indicated that bluegill significantly reduced densities of these prey taxa in the absence of the fish assemblage, but the effects were not significant in the presence of the fish assemblage. The shift from significant bluegill effects in the absence of the fish assemblage to non-significant effects in the presence of the fish assemblage was probably due to the presence of other fish species in the community that are trophically or functionally similar to bluegill (Power et al. 1996). While we did not determine the individual impacts of mosquito-

fish and common carp, both are carnivores that reduce densities of zooplankton and macroinvertebrates (Hurlbert et al. 1972; Hurlbert and Mulla 1981; Richardson et al. 1990; Cline et al. 1994). In our study, the presence of the fish assemblage had effects similar to bluegill on invertebrates and reduced densities of *Daphnia*, *Ceriodaphnia*, cyclopoid copepodids, copepod nauplii (Fig. 1), gastropods, and notonectids (Fig. 2). Consequently, bluegill failed to have significant effects in the presence of the fish assemblage because prey were already suppressed to near non-existent levels by the fish assemblage.

In their review of the keystone species concept, Menge et al. (1994) cited Hall et al. (1970) as an example of an experiment in which bluegill acted as a keystone species. However, Hall et al. (1970) examined the effects of bluegill on invertebrate and algal communities only in the absence of other fish species. It has been hypothesized that the effects of a keystone consumer may be context dependent (Menge et al. 1994), or dependent on a variety of biotic and abiotic factors which may modify their effects (Power et al. 1996). One factor that may underlie the context dependency of a species is the presence of other consumers in the food web that are trophically or functionally similar (Power et al. 1996). The higher the number of species in a food web that are trophically similar to the keystone species, the greater the chance the species will not play a keystone role (Menge and Sutherland 1987; Power et al. 1996). Our results suggest that bluegill may not function as a keystone species in lakes with complex assemblages composed of other zooplanktivorous and benthivorous fish species.

Although some ecologists claim microcosm experiments have limited relevance for community ecology research (Carpenter and Kitchell 1992; Carpenter 1996, 1999), others view microcosms as useful tools for exploring ecological interactions (Levin 1992; Wilbur 1997; Drenner and Mazumder 1999; Huston 1999). We recognize that the experiment presented here had limitations. The small size of the mesocosms did not allow us to assess niche shifts, resource partitioning, and habitat selection of the fish species in the community (Werner and Hall 1976, 1988; Werner et al. 1983; Mittelbach and Osenberg 1993). Furthermore, the fish assemblage treatment in this experiment was composed of only two fish species, which does not reflect the species complexity of large North American lakes (Griffiths 1997). However, the use of small microcosms allowed us to examine experimentally whether the effects of bluegill were different in the presence and absence of other fish species. The results of this experiment indicate that the effects of bluegill are context dependent, or dependent upon the presence of other fish species, and we hypothesize that bluegill may not function as a keystone species in lakes with complex fish assemblages.

Acknowledgements We would like to thank the Tarrant Regional Water District for use of the fish hatchery and Kirk Guckenberger and Judson Smith for assistance in the field. This research was supported by TCU RF grant no. 5-23610 and a TCU Adkins Fellowship to Graduate Students.

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