

Primary Research Paper

Gape limitation, prey size refuges and the top–down impacts of piscivorous largemouth bass in shallow pond ecosystems

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Abstract

Top–down control of phytoplankton biomass through piscivorous fish manipulation has been explored in numerous ecological and biomanipulation experiments. Piscivores are gape-limited predators and it is hypothesized that the distribution of gape sizes relative to distribution of body depths of prey fish may restrict piscivore effects cascading to plankton. We examined the top–down effects of piscivorous largemouth bass on nutrients, turbidity, phytoplankton, zooplankton and fish in ponds containing fish assemblages with species representing a range of body sizes and feeding habits (western mosquitofish, bluegill, channel catfish, gizzard shad and common carp). The experimental design consisted of three replicated treatments: fishless ponds (NF), fish community without largemouth bass (FC), and fish community with largemouth bass (FCB). Turbidity, chlorophyll *a*, cyclopoid copepodid and copepod nauplii densities were significantly greater in FC and FCB ponds than in NF ponds. However, these response variables were not significantly different in FC and FCB ponds. The biomass and density of shallow-bodied western mosquitofish were reduced and bluegill body depths shifted toward larger size classes in the presence of largemouth bass, but the biomass and density of all other fish species and of the total fish community were unaffected by the presence of largemouth bass. Our results show that top–down impacts of largemouth bass in ecosystems containing small- and deep-bodied fish species may be most intense at the top of the food web and alter the size distribution and species composition of the fish community. However, these top–down effects may not cascade to the level of the plankton when large-bodied benthivorous fish species are abundant.

Introduction

As top consumers in freshwater ecosystems, piscivorous fish have direct and indirect impacts that alter the biota and water quality of lakes. This top–down effect has been termed the trophic cascade (Carpenter et al., 1985) or cascading trophic interactions theory (CTI theory – *sensu* Elser et al., 1998). Current models of the top–down impacts of piscivores in lake systems predict that an increase

in piscivore biomass will reduce the biomass of zooplanktivorous and benthivorous fish, leading to a reduction in phytoplankton biomass (Carpenter et al., 1985; Jeppesen et al., 1997; 2003; Benndorf et al., 2002). The top–down control of algal biomass in lakes has become a widely accepted ecological paradigm (Pace et al., 1999; Polis et al., 2000) and the enhancement of piscivore populations is a water quality management technique that has been attempted in numerous

biomanipulation studies (Shapiro, 1990; Reynolds, 1994; McQueen, 1998; Drenner & Hambright, 1999).

Some ecologists have questioned the generality of top-down trophic cascade models and their applicability to food webs. McQueen et al. (1986) hypothesized that piscivore effects are strongest at the top of food webs and dissipate at lower trophic levels. This dampening of top-down trophic level effects is consistent with results of experimental investigations of fish effects in freshwater ecosystems (DeMelo et al., 1992; Shurin et al., 2002). Polis & Strong (1996) questioned top-down trophic level effects, suggesting that food webs may be too complex to show trophic level mediated patterns. They postulated that trophic cascades are uncommon, "exceptions that prove the rule," and that a major challenge in ecology is to determine which systems are susceptible to top-down control (but see Hairston & Hairston, 1993, 1997).

In freshwater ecosystems, the vulnerability of prey fish assemblages to piscivore predation is a potential mechanism limiting the top down effects of piscivores in food webs (Hambright et al., 1986, 1991; Hambright, 1994). Piscivore mouth gape size restricts the sizes and composition of prey fish that piscivores can ingest (Hoyle & Keast, 1987, 1988; Mittelbach & Persson, 1998). Hambright et al. (1991) predicted that, due to the gape limitation of piscivores, the top-down effects of piscivores observed in lakes containing fish assemblages dominated by deep-bodied fish species may be different from top-down piscivore effects observed in lakes dominated by small, shallow-bodied fish species. Hambright (1994) further suggested that in systems where the fish assemblage contains both shallow- and deep-bodied individuals, piscivore predation may lead to the dominance of larger-bodied and invulnerable individuals in the community, thus preventing the effects of piscivores from cascading to phytoplankton. It was further hypothesized that intense piscivore-mediated trophic cascades may not be apparent in lower-latitude limnetic ecosystems in North America because deep-bodied omnivorous fish often dominate the fish assemblages (Stein et al., 1995). Despite the implications of these predictions for the prospect of top-down control of lower-latitude limnetic ecosystems in North America, there has been relatively little direct experimental or

empirical assessment of these hypotheses (see Dettmers et al., 1996).

In this paper, we evaluated the predictions of Hambright (1994) and Stein et al. (1995) by examining the top-down effects of piscivorous largemouth bass (*Micropterus salmoides*) in experimental ponds containing fish assemblages composed of both deep- and shallow-bodied species. Largemouth bass is found in most of North America (Miranda, 1983; Page & Burr, 1991) and has been introduced worldwide (Welcomme, 1988). The top-down effects of largemouth bass have been examined in several trophic cascade studies (see Drenner & Hambright, 2002 for review), but the present study is one of the few to experimentally assess the top-down effects of largemouth bass in systems containing fish species that vary in body morphologies and feeding preferences (but see Hambright, 1994).

Materials and methods

The study was conducted in 11 ponds at the Eagle Mountain Fish Hatchery, Fort Worth, Texas, USA. Ponds ranged in surface area from 0.18 to 0.56 ha with a maximum depth of 1.2 m and a mean depth of 0.6 m. Ponds had earthen bottoms and contained the macrophytes bushy pond weed (*Najas guadalupensis*), musk grass (*Chara* spp.), pondweeds (*Potamogeton pusillus* and *P. nodosus*), American lotus (*Nelumbo lutea*), Eurasian water milfoil (*Myriophyllum spicatum*) and coontail (*Ceratophyllum demersum*).

The experimental design consisted of three treatments, each with 3 or 4 replicates: (1) ponds with no fish (NF; $n=3$), (2) ponds with a fish community without largemouth bass (FC; $n=4$), and (3) ponds with a fish community containing largemouth bass (FCB; $n=4$). The fish community was composed of western mosquitofish (*Gambusia affinis*), bluegill (*Lepomis macrochirus*), channel catfish (*Ictalurus punctatus*), gizzard shad (*Dorosoma cepedianum*) and common carp (*Cyprinus carpio*). These fish species were selected because their North American range distributions overlap with largemouth bass (Page & Burr, 1991), are members of different feeding guilds in freshwater fish communities and represent a range of small- and deep-bodied morphologies found in

many fish communities in Texas and the southern United States (Miranda, 1983). Initial stocking rates and biomass distribution of these species in the fish community were intended to reflect the dominance of deep-bodied benthivorous and omnivorous taxa in many Texas and southern United States limnetic fish communities (Jenkins, 1975; Miranda, 1983). Western mosquitofish feed primarily on zooplankton and macroinvertebrates (Hurlbert et al., 1972; Hurlbert & Mulla, 1981; Lancaster & Drenner, 1990; Drenner & Smith, 1991). Bluegill are carnivores that consume zooplankton and macroinvertebrates (Hall et al., 1970; Drenner et al., 1990; Nowlin & Drenner, 2000). Channel catfish are carnivores that consume benthic invertebrates and occasionally fish (Cline et al., 1994). Gizzard shad are omnivores that primarily consume benthic detritus (Schaus et al., 2002). Common carp are carnivores that consume benthic invertebrates (Qin & Threlkeld, 1990; Richardson et al., 1990). Because of their small shallow minnow-like body, western mosquitofish are highly vulnerable to piscivory even as adults. Bluegill, channel catfish, gizzard shad and common carp may be vulnerable to largemouth bass predation as juveniles, but are capable of reaching a predation refuge through large adult body size (Werner & Hall, 1988; Hambright et al., 1991).

Ponds were filled and water levels were maintained throughout the experiment with water from nearby eutrophic Eagle Mountain Lake. Adult fish of each species were stocked into ponds from 6 June 1995 to 15 July 1995 at biomasses based on average ichthyomasses of feeding guilds in Texas reservoirs (Miranda, 1983). Largemouth bass, mosquitofish, bluegill, channel catfish, gizzard shad and common carp were stocked at 21.2, 1.7, 43.7, 18.6, 78.2 and 69.7 kg ha⁻¹, respectively. Largemouth bass stocking rate was based upon Miranda's (1983) "black bass" biomass, mosquitofish were stocked at the biomass of "minnows", bluegill stocking rate was based upon "sunfish" biomass and gizzard shad were stocked at the biomass of "gizzard shad". Channel catfish stocking rate was based upon the combined "blue catfish" and "channel catfish" biomass and common carp stocking rate was based upon the combined biomass of "carp and goldfish", "carp-suckers" and "suckers". Liquid commercial fertilizer (9.4 L ha⁻¹ of 10N:34P:0K) was added to

each pond by surface broadcasting every 4–6 weeks from 13 August 1995 through 8 June 1996, to maintain eutrophic conditions throughout the experiment. These conditions were maintained because top-down fish effects are predicted to be more apparent in eutrophic systems (Mazumder, 1994a; Jeppesen et al., 1997, 2003; Drenner & Hambright, 2002; but see DeMelo et al., 1992; Benndorf et al., 2002; Borer et al., 2005).

Ponds were sampled every 4–6 weeks from 23 July 1995 to 29 June 1996 for temperature, total phosphorus (TP) and total nitrogen (TN), turbidity and chlorophyll *a* (Chl *a*) at the deepest point in each pond. Temperature was measured with a YSI Model 57 temperature/dissolved oxygen meter (Yellow Springs Instruments, Inc., Yellow Springs, OH, USA). Water for nutrients, turbidity and Chl *a* was collected with a PVC integrated tube sampler. Samples for TP were digested with potassium persulfate (Menzel & Corwin, 1965) and analyzed with the malachite green method (Van Veldhoven & Mannaerts, 1987). Samples for TN were digested with alkaline potassium persulfate (D'Elia et al., 1977) and absorbance was measured at 220 nm [American Public Health Association (APHA), 1985]. Turbidity was determined on a Hach 2100A turbidimeter. Chl *a* samples were filtered onto Millipore HAWP membrane filters (0.45 μm pore size), wrapped in aluminum foil and frozen. Chl *a* was extracted in 2:1 chloroform:methanol in the dark at room temperature for at least 4 h and absorbance was read at 665 nm (Wood, 1985). Zooplankton were collected by a vertical tow of the entire water column with a 12 cm diameter 80 μm Wisconsin plankton net. Samples were preserved in 10% sucrose formalin (Haney & Hall, 1973) and counted on a dissecting microscope. Cladocerans were identified to genus and copepod copepodids were identified to order (calanoid or cyclopoid). Copepod nauplii and rotifers (identified to genus) were also enumerated.

To assess fish populations in the presence and absence of largemouth bass, ponds were drained from 1 to 20 March 1997 by opening a valve in a concrete box located at the deepest end of each pond. Water drained into the box and passed through a 1.5-mm mesh screen to prevent loss of fish. As the pond drained, fish were netted out of the concrete box and placed into holding tanks.

Total lengths (TL) were taken for all fish. To expedite data collection, mass (g) and body depth (cm) measurements were taken from a sub-set of 8–87 individual fish (>4 cm TL) of each species in each pond. These sub-sets of fish represented the range of size classes of each species in each pond and were used to create pond-specific length–mass and length–body depth regressions for each species. Mass and body depths of individual fish >4 cm TL of each species was estimated from these length–mass and length–body depth regressions. When ponds were drained and fish were removed, we observed that all western mosquitofish and small bluegill <4 cm TL had body depths <1 cm. Therefore, we grouped all western mosquitofish and bluegill <4 cm TL by species into aliquots of 50 individuals and mass (g) was determined in bulk. The gape sizes of individual largemouth bass (cm) were calculated from the equation of Johnson & Post (1996), in which largemouth bass gape widths are predicted from fish TL.

Data were analyzed with SYSTAT (Wilkinson, 1998). Water temperature, TP, TN, turbidity, Chl *a* and zooplankton densities over the experimental period were analyzed with one-way repeated measures ANOVA. If a significant overall treatment effect was detected, *post hoc* paired comparisons were performed between treatments across all dates (NF vs FC, NF vs FCB, FC vs FCB) with one-way repeated measures ANOVA. If a significant time \times treatment interaction was detected (indicating interdependence of time and the treatment effect), we tested for differences between treatments (NF, FC and FCB) on each sampling date using one-way ANOVAs. To evaluate the effects of largemouth bass on the fish community, total densities (number ha⁻¹) and total biomasses (kg ha⁻¹) of all fish (excluding largemouth bass) in FC and FCB ponds were compared with Student's *t*-test. To examine the effects of largemouth bass on the biomass and density of individual fish species in the fish community, FC and FCB ponds were compared with Student's *t*-test. Significance was inferred at $p \leq 0.05$ for all analyses.

Results

Water temperature in ponds varied from a high of 31 °C in July 1995 and 1996 to a low of 6°

in January 1996 (Fig. 1a). Repeated measures ANOVA detected a marginally significant treatment effect on water temperature ($p=0.06$). Examination of our data indicated that two of the four FCB ponds exhibited slightly lower water temperatures (~ 2.3 °C cooler) than all other ponds during summer (July–August 1995 and May–June 1996), thus contributing to the marginally significant treatment effect. During summer, these two ponds had high densities of the broad-leafed emergent macrophyte American lotus and we hypothesize that shading by this macrophyte might have contributed to the slightly lower water temperatures.

There was no significant treatment effect on TP ($p=0.32$; Fig. 1b) or TN concentration ($p=0.30$; Fig. 1c). TP in ponds ranged from 20 to 125 $\mu\text{g L}^{-1}$ and TN ranged from 200 to 1500 $\mu\text{g L}^{-1}$, indicating eutrophic conditions throughout the experiment (Wetzel, 1983; Kalff, 2002).

The repeated measures ANOVA detected a significant treatment effect on turbidity ($p=0.02$; Fig. 1d). *Post hoc* comparison of treatments indicated that FC ($p=0.01$) and FCB ($p=0.02$) ponds were consistently more turbid than NF ponds throughout the experimental period. The turbidity of FC and FCB ponds did not differ significantly from one another ($p=0.74$).

The repeated measures ANOVA detected a significant treatment effect on Chl *a* concentration ($p=0.02$; Fig. 1e) and a significant treatment \times time interaction ($p=0.01$). Pair-wise comparisons between treatments across all dates indicated that FC ($p=0.01$) and FCB ponds ($p=0.03$) had significantly higher Chl *a* concentrations than NF ponds, but FC and FCB ponds did not differ significantly ($p=0.67$). Because a significant treatment \times time interaction effect was detected, we performed pair-wise comparisons between treatments on individual sampling dates. FC ponds had significantly greater Chl *a* concentrations than NF ponds in August ($p=0.008$), October ($p=0.04$) and November 1995 ($p=0.003$). FCB ponds had significantly greater Chl *a* than NF ponds on July 1995 ($p=0.025$), August 1995 ($p=0.047$), April 1996 ($p=0.015$) and May 1996 ($p=0.050$). Chl *a* in FCB ponds exhibited a marginally significant enhancement ($p=0.055$) over FC ponds on one sampling date (March 1996).

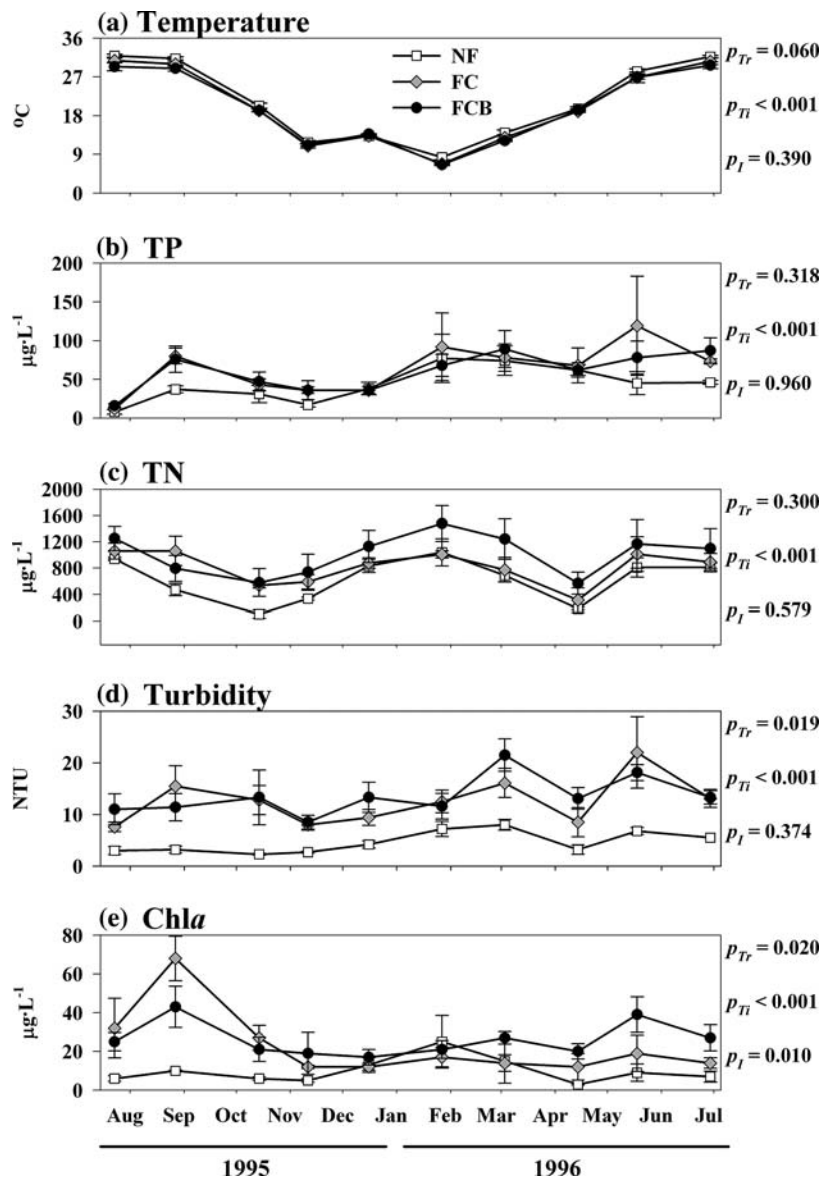


Figure 1. Temporal responses of (a) water temperature, (b) TP, (c) TN, (d) turbidity and (e) chlorophyll *a* in the three experimental treatments from July 1995–July 1996. p -values of the repeated measures ANOVA for the overall treatment effect (p_{Tr}), the time effect (p_{Ti}) and the treatment \times time interaction effect (p_I) are presented for each response variable on the right-hand side of each panel. Error bars represent ± 1 SE.

Inspection of Chl *a* data over the experiment indicated Chl *a* concentration in NF ponds and ponds that contained fish (FC and FCB ponds) only significantly differed from one another when water temperatures were > 11 $^{\circ}\text{C}$ (Fig. 1 and results of the date-by-date Chl *a* analyses). To further explore the relationship between differences in Chl *a* concentration among treatments and water

temperature, differences in Chl *a* concentration in NF ponds versus FC and FCB ponds (FC Chl *a* concentration minus NF Chl *a* concentration, and FCB Chl *a* concentration minus NF Chl *a* concentration) were plotted as a function of water temperature (Fig. 2). In both FC and FCB ponds, Chl *a* difference significantly increased with water temperature, indicating that the magnitude of fish

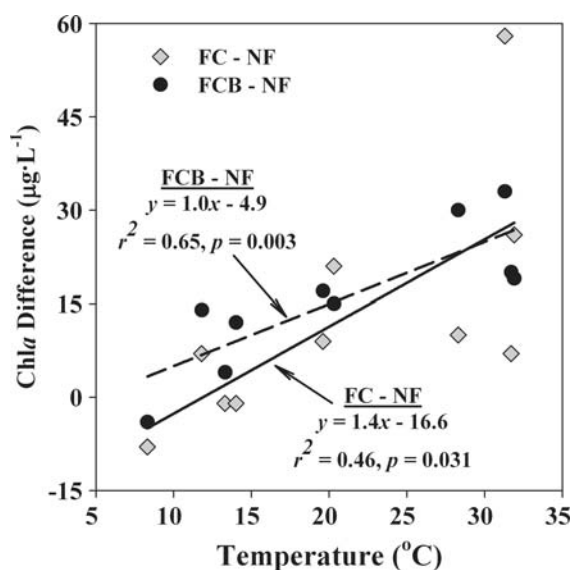


Figure 2. Difference in Chl *a* concentration in ponds with the fish assemblage only (FC), ponds with the fish assemblage + largemouth bass (FCB), and fishless ponds (NF) as a function of water temperature. Difference was calculated by subtracting the mean NF Chl *a* concentration from the mean FC or mean FCB Chl *a* concentration on each sampling date. Regression equations and statistical results are presented for each analysis (FC–NF and FCB–NF). The combined FC and FCB regression line, equation and statistical results are not presented in the figure ($y = 1.2x - 10.8$; $r^2 = 0.50$; $p < 0.001$).

effects on Chl *a* was a significant positive function of water temperature (Fig. 2). In addition, the Chl *a* difference–water temperature relationships did not significantly differ between FC and FCB ponds (ANCOVA, $F_{9,1} = 4.69$, $p = 0.453$). When FC–NF and FCB–NF points are combined and linear regression analysis is performed, Chl *a* difference remains a significant positive function of water temperature ($y = 1.2x - 10.8$; $r^2 = 0.50$; $p < 0.001$).

Repeated measures ANOVA detected an overall treatment effect on cyclopoid copepodids ($p = 0.04$; Fig. 3a) and copepod nauplii ($p = 0.01$; Fig. 3b) densities. *Post hoc* comparisons revealed that densities of cyclopoid copepodids and copepod nauplii were significantly higher in FC ($p = 0.03$) and FCB ($p = 0.003$) ponds than NF ponds over the experiment, but densities were not significantly different between FC and FCB ponds (cyclopoid copepodids $p = 0.08$; nauplii $p = 0.935$). Repeated measures ANOVA also detected a marginally significant treatment effect on *Daphnia* spp. (Fig. 3c; $p = 0.082$). We further explored this marginal treatment effect on *Daphnia* because

large cladoceran grazers such as *Daphnia* are critical contributors to the top–down control of phytoplankton biomass (Mazumder, 1994a, b, c). When *post hoc* comparisons were performed, FC ponds had significantly higher *Daphnia* densities than NF ponds ($p = 0.014$), but FCB ponds and NF ponds did not significantly differ ($p = 0.100$), nor did *Daphnia* densities significantly differ in FC and FCB ponds throughout the experiment ($p = 0.157$). Densities of *Bosmina* sp. ($p = 0.206$), *Ceriodaphnia* sp. ($p = 0.103$), *Diaphanosoma brachyurum* ($p = 0.118$), calanoid copepods ($p = 0.251$), and non-predatory rotifers ($p = 0.646$) did not significantly differ between treatments and are not presented in Figure 3.

We evaluated the effects of largemouth bass on the composition, biomass and size structure of fish communities through comparison of the biomass and density of the entire fish assemblage (excluding largemouth bass), as well as the individual fish species in FC and FCB ponds after the experiment. The presence of largemouth bass did not have a significant effect on total fish community biomass or density (Fig. 4a). The presence of largemouth bass significantly reduced the biomass and density of western mosquitofish (Fig. 4c), but had no effect on the biomass and density of bluegill (Fig. 4d), channel catfish (Fig. 4e), gizzard shad (Fig. 4f) and common carp (Fig. 4g). In both FC and FCB ponds, common carp represented the largest contributor to total fish community biomass, accounting for 57–82% of the biomass at the end of the experiment.

To determine if fish species occupied a size refuge from predation due to gape-limitation of largemouth bass, the frequency distributions of largemouth bass gape sizes and the body depths of individual fish species were compared. Largemouth bass gapes ranged from <1 to 6 cm, with the greatest proportion of largemouth bass biomass in the 5 cm size class (Fig. 5a). All western mosquitofish had body depths ≤ 1 cm in both treatments, were vulnerable to largemouth bass predation and are not presented in Figure 5. In both treatments, bluegill body depths ranged from 1 to 8 cm (Fig. 5b). However, there was a shift in the body depth size distribution of bluegill when FC and FCB ponds were compared. Bluegill in FCB ponds had a higher proportion of deeper-bodied size classes (between 5 and 8 cm), whereas bluegill

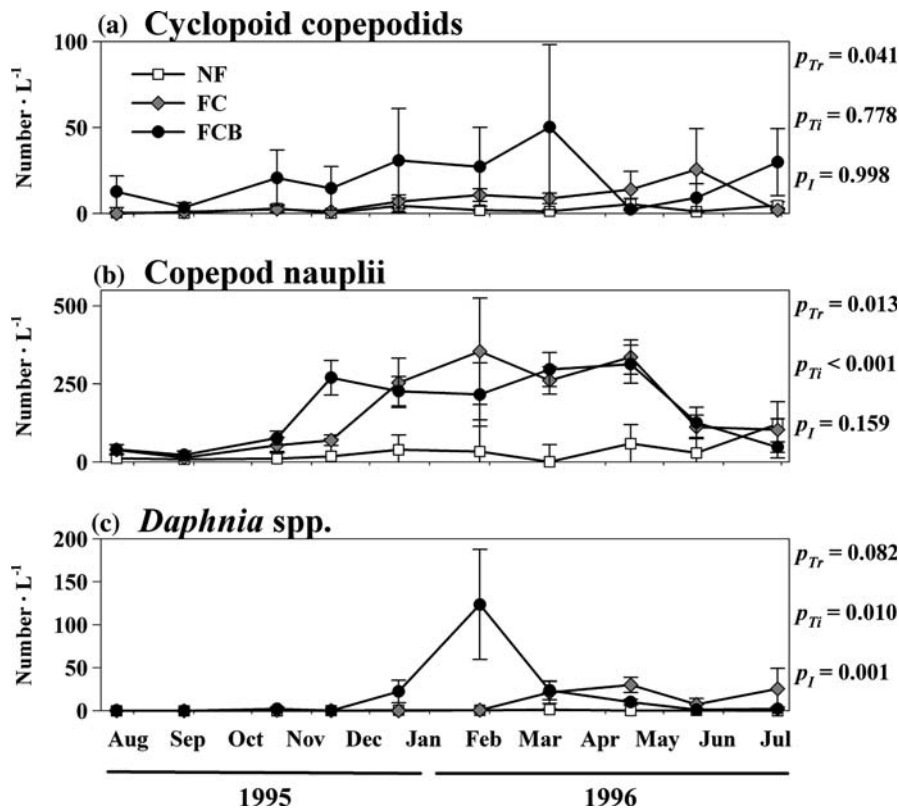


Figure 3. Temporal responses of (a) cyclopoid copepodids, (b) copepod nauplii and (c) *Daphnia* spp. in the three experimental treatments from July 1995 – July 1996. p -Values of the repeated measures ANOVA for the overall treatment effect (p_{Tr}), the time effect (p_{Ti}) and the treatment \times time interaction effect (p_I) are presented for each response variable on the right-hand side of each panel. Temporal responses of *Bosmina* sp., *Ceriodaphnia* sp., *Diaphanosoma brachyurum*, calanoid copepods and non-predatory rotifers are not presented because these zooplankton taxa did not exhibit significant treatment effects. Error bars represent ± 1 SE.

biomass in FC ponds had the largest proportion of biomass in the 2 cm body depth size class (Fig. 5b). Channel catfish body depths ranged from 5 to 10 cm both in the presence and absence of largemouth bass, with the highest proportion of biomass in the 6–9 cm size classes in both treatments (Fig. 5c). In FCB and FC ponds, gizzard shad body depths ranged from 7 to 13 cm, and were therefore invulnerable to largemouth bass predation (Fig. 5d). Common carp occupied a body depth size refuge from largemouth bass predation in both treatments with body depths ranging from 6 to 22 cm, with the majority of the biomass in both treatments in size classes >12 cm (Fig. 5e).

Discussion

In the study presented here, the presence of largemouth bass altered the composition and size

distribution of the fish community. Although total fish community biomass and density were unaffected by the presence of largemouth bass, the density and biomass of western mosquitofish was significantly lower in the presence of largemouth bass. We further observed that the total density and biomass of bluegill were not different in the presence and absence of largemouth bass, but bluegill populations in FCB ponds exhibited body depth distributions skewed toward larger size classes when compared to bluegill populations in FC ponds. The reduction of small-bodied individuals from the fish communities in ponds containing largemouth bass is consistent with predictions and observations of fish community responses to gape-limited piscivore predation (Hambricht et al., 1986, 1991; Tonn & Paszkowski, 1986; Tonn et al., 1992; Hambricht, 1994; Findlay et al., 2000).

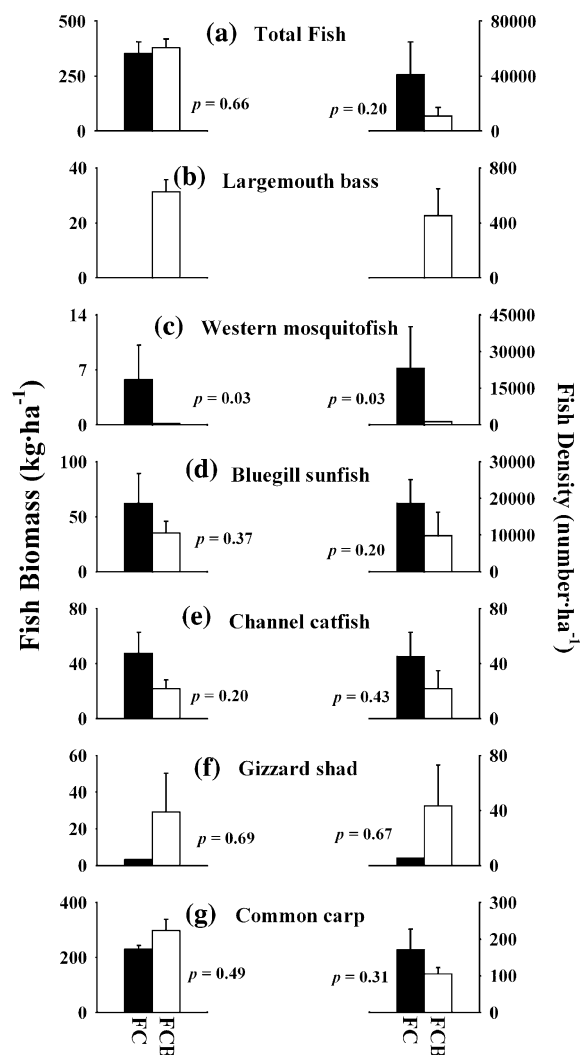


Figure 4. Biomass (kg ha^{-1}) and density (number ha^{-1}) of fish in FC and FCB ponds at the end of the experiment. (a) Total fish (excluding largemouth bass), (b) largemouth bass, (c) western mosquitofish, (d) bluegill sunfish, (e) channel catfish, (f) gizzard shad, and (g) common carp. Error bars represent ± 1 SE. p -Values from Student's t -tests comparing FC and FCB ponds for each response variable are given on individual panels. Note that y -axis scales differ between species.

We found no evidence of the effects of largemouth bass cascading to the plankton community; thus our results appear to be consistent with the prediction of McQueen et al. (1986) that piscivore effects are most intense at the top of the food web and are relatively weak at lower trophic levels. We did not observe significantly higher zooplankton densities when largemouth bass was present in the fish community. Densities of cyclopoid copepodids

and copepod nauplii were higher in FC and FCB ponds than in NF ponds, but FC and FCB ponds did not differ from each other. Similarly, *Daphnia* exhibited a marginally significant treatment effect, but *Daphnia* densities did not differ in FC and FCB ponds. In addition, phytoplankton biomass (Chl *a*) was significantly higher in ponds that contained fish, but did not significantly differ between FC and FCB ponds. Chl *a* is one of the most commonly used measurements of phytoplankton biomass and most trophic cascade models predict comparatively lower phytoplankton biomass in systems containing piscivores (Carpenter et al., 1985; Benndorf et al., 2002; Drenner & Hambright, 2002). However, a number of studies have found that the top-down impacts of piscivores may alter the species composition of the phytoplankton community, leaving total phytoplankton biomass unaffected (Tremmel et al., 2001; Benndorf et al., 2002; Drenner et al., 2002). In this study, we did not assess the species composition of the phytoplankton community; therefore, we do not know whether the phytoplankton community composition was significantly different among experimental treatments.

We postulate that the body size distribution and species composition of the fish communities in our experiment may account for the lack of effects of largemouth bass cascading to the plankton. Fish species which are partially or almost exclusively benthivorous and capable of obtaining a size refuge from piscivory (bluegill, channel catfish, gizzard shad and common carp) dominated the fish community biomass in both FC and FCB ponds. Benthivorous fish increase turbidity through sediment resuspension (Meijer et al., 1990; Havens, 1993; Breukelaar et al., 1994; Tátrai et al., 1997), excrete benthically derived nutrients into the water column (Lamarra, 1975; Brabrand et al., 1990; Schaus et al., 1997) and increase phytoplankton biomass (Qin & Threlkeld, 1990; Richardson et al., 1990; Tátrai et al., 1990; Drenner et al., 1998). In our study, differences in Chl *a* concentration between ponds that contained fish (FC and FCB) and fishless ponds (NF) only occurred during the warmer portions of the year. In a pond experiment investigating the synergistic effects of nutrients and benthivorous fish (common carp), Drenner et al. (1998) found that fish-nutrient interaction effects on Chl *a* were only

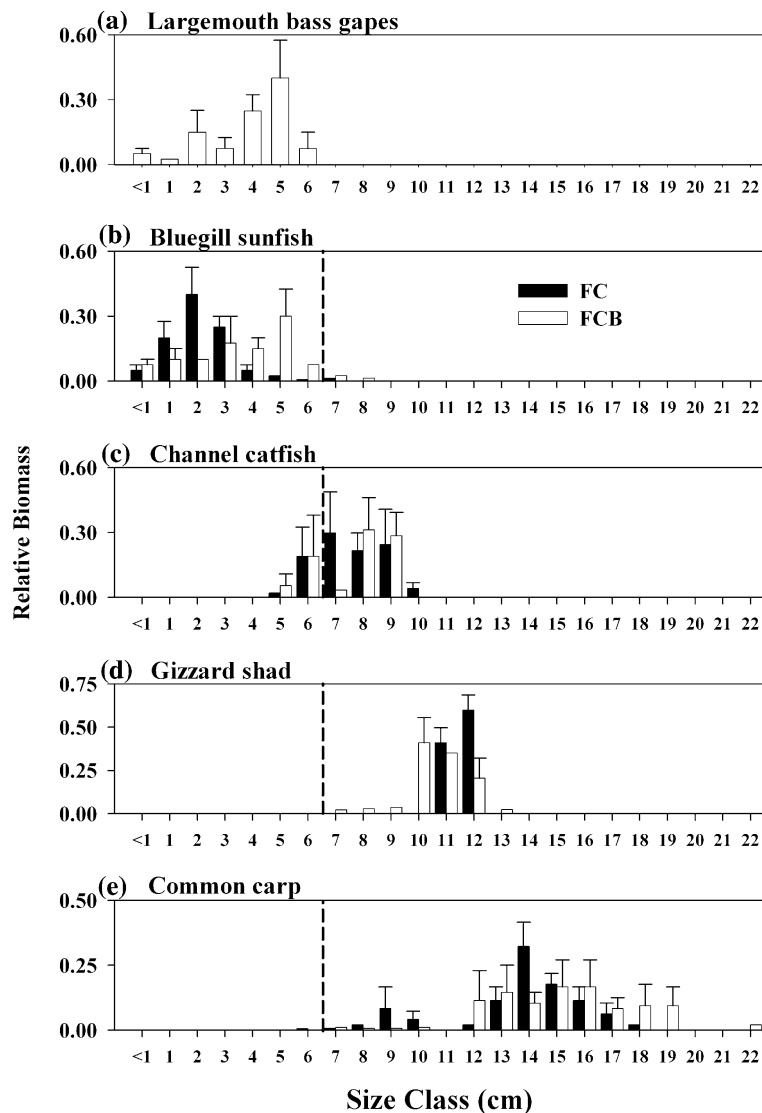


Figure 5. Size distributions of largemouth bass gapes and body depths of fish species in ponds after the end of the experiment. (a) The distribution of largemouth bass gapes in 1 cm size class increments in FCB ponds. (b) The biomass distribution of bluegill in 1 cm body depth size class increments in FC and FCB ponds. (c) channel catfish, (d) gizzard shad and (e) common carp. Western mosquitofish are not presented because all body depths were <1 cm in FC and FCB ponds. Error bars are ± 1 SE. The vertical dashed lines in panels (b) through (e) represent the maximum observed largemouth bass gapes (6 cm).

observed during summer. Our results appear to support the hypothesis that the impacts of benthivores may be greater during periods of relatively warmer water temperature, when the feeding activity of fish is higher, and indicate that these effects may not be impacted by the presence of gape-limited piscivores.

We searched the published literature to find studies that examined the top-down effects of

largemouth bass cascading to phytoplankton. In our review of the literature, we found a large number of studies in which largemouth bass were simultaneously stocked with other piscivores or in conjunction with other ecosystem manipulations, such as human removal of fish, thus making the effects of largemouth bass indistinguishable from those of the other experimental manipulations (Hrbáček et al., 1961; Shapiro & Wright, 1984;

Wagner, 1986; Carpenter et al., 1987, Hanson & Butler, 1990; Hanson & Butler, 1994a, b; McQueen et al., 2001; Albright et al., 2004). Six studies examined the top-down effects of largemouth bass cascading to phytoplankton without additional manipulations or simultaneous stocking with other piscivore species (Spencer & King, 1984; Hambright et al., 1986; Turner & Mittelbach, 1990; Hambright, 1994; Baca & Drenner 1995; Mittelbach et al., 1995; Drenner et al., 2002). Four studies were conducted in experimental ponds (Spencer & King, 1984; Hambright et al., 1986; Turner & Mittelbach, 1990; Hambright, 1994) and two studies involved the introduction of largemouth bass to whole lakes (Baca & Drenner, 1995; Mittelbach et al., 1995; Drenner et al., 2002). Two experimental pond studies (Spencer & King, 1984; Hambright, 1994) detected a decline in or comparatively lower phytoplankton biomass in the presence of largemouth bass. Mittelbach et al. (1995) found an increase in water clarity (used as a surrogate for phytoplankton biomass) after the reintroduction of largemouth bass into Wintergreen Lake. Fish communities of these three studies were dominated by or contained shallow-bodied fish species, such as fathead minnow (*Pimephales promelas*), golden shiner (*Notomigonus crysoleucas*) and brook stickleback (*Culaea inconstans*). The three remaining studies found no impact of largemouth bass cascading to phytoplankton biomass (Hambright et al., 1986; Turner & Mittelbach, 1990; Baca & Drenner, 1995; Drenner et al., 2002). Prey fish assemblages in the studies by Hambright et al. (1986) and Turner & Mittelbach (1990) were composed entirely of bluegill sunfish, and the fish community of the Balancing Reservoirs study (Baca & Drenner, 1995, Drenner et al., 2002) was dominated by threadfin shad (*Dorosoma petenense*), but also contained gizzard shad, various cyprinids and sunfishes (*Lepomis* spp.).

The trophic cascade impacts of consumers have received considerable attention from ecologists working in freshwater, marine and terrestrial ecosystems (Pace et al., 1999; Schmitz et al., 2000; Shurin et al., 2002; Borer et al., 2005). Ecologists have observed that top consumers in food webs can have strong impacts on ecosystem processes, leading to the conclusion that these top consumers may function as keystone species, or species that

have impacts disproportionately large in relation to their abundance or biomass (Power et al., 1996). Largemouth bass is considered a keystone species (Mittelbach et al., 1995; Power et al., 1996; Schindler et al., 1997), due, in part, to the results from studies examining its trophic cascade effects. Some ecologists have questioned the overall utility of the keystone species concept (Hurlbert, 1997; Bond, 2001), while others have proposed that the effects of consumers are context dependent, or dependent upon abiotic and biotic factors in the ecosystem (Menge et al., 1994; Nowlin & Drenner, 2000). For example, the effects of a fish species can be dampened or masked by the effects of other fish species in the community (Nowlin & Drenner, 2000). The results of our study indicate that the role of largemouth bass as a keystone predator in ecosystems may be dependent upon the species composition and size distribution of the fish community. In shallow lentic ecosystems containing fish communities dominated by large-bodied benthivorous fish species, the effects of largemouth bass may be most apparent at the top of the food web and minimal at the level of the plankton.

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References

- Albright, M. F., W. N. Harman, W. T. Tibbits, M. S. Gray, D. M. Warner & R. J. Hamway, 2004. Biomanipulation: a classic example in a shallow eutrophic pond. *Lake and Reservoir Management* 20: 181–187.
- APHA., 1985. Standard Methods for the Examination of Water and Wastewater (16th edn.) American Water Works Association, Washington, DC.
- Baca, R. M. & R. W. Drenner, 1995. Do the effects of piscivorous largemouth bass cascade to the plankton? *Hydrobiologia* 316: 139–151.
- Benndorf, J., W. Böing, J. Koop & I. Neubauer, 2002. Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. *Freshwater Biology* 47: 2282–2295.
- Bond, W., 2001. Keystone species – hunting the snark? *Science* 292: 63–64.

- Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper & B. S. Halpern, 2005. What determines the strength of a trophic cascade? *Ecology* 86: 528–537.
- Brabrand, A., B. A. Faafeng & J. P. M. Nilssen, 1990. Relative importance of phosphorus supply to phytoplankton – fish excretion versus external loading. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 364–372.
- Breukelaar, A. W., E. H. R. R. Lammens, J. G. P. K. Breteker & I. Tatrai, 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll-a. *Freshwater Biology* 32: 13–121.
- Carpenter, S. R., J. Kitchell & J. Hodgson, 1985. Cascading trophic interactions and lake productivity. *BioScience* 35: 634–639.
- Carpenter, S. R., J. F. Kitchell, J. R. Hodson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He & C. N. Von Ende, 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68: 1863–1867.
- Cline, J. M., T. L. East & S. T. Threlkeld, 1994. Fish interactions with the sediment-water interface. *Hydrobiologia* 275/276: 301–311.
- D'Elia, C. F., P. A. Steudler & N. Corwin, 1977. Determination of total nitrogen in aqueous samples using persulfate digestion. *Limnology and Oceanography* 22: 760–764.
- DeMelo, R., R. France & D. J. McQueen, 1992. Biomanipulation: hit or myth? *Limnology and Oceanography* 37: 192–207.
- Drenner, R. W. & K. D. Hambright, 1999. Biomanipulation of fish assemblages as a lake restoration technique. *Archiv für Hydrobiologie* 146: 129–165.
- Drenner, R. W. & K. D. Hambright, 2002. Piscivores, trophic cascades, and lake management. *The Scientific World* 2: 284–307.
- Drenner, R. W. & J. D. Smith, 1991. Biomass-dependent effects of mosquitofish on zooplankton, chlorophyll and size distribution of particulate phosphorus. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen* 24: 2382–2386.
- Drenner, R. W., J. D. Smith, J. R. Mummert & H. F. Lancaster, 1990. Responses of a eutrophic pond community to separate and combined effects of N:P supply and planktivorous fish: a mesocosm experiment. *Hydrobiologia* 208: 161–167.
- Drenner, R. W., K. L. Gallo, R. M. Baca & J. D. Smith, 1998. Synergistic effects of nutrient loading and omnivorous fish on phytoplankton biomass. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 2087–2096.
- Drenner, R. W., R. M. Baca, J. S. Gilroy, M. R. Ernst, D. J. Jensen & D. H. Marshall, 2002. Community responses to piscivorous largemouth bass: a biomanipulation experiment. *Lake and Reservoir Management* 18: 44–51.
- Elser, J. J., T. H. Chrzanowski, R. W. Sterner & K. H. Mills, 1998. Stoichiometric constraints on food-web dynamics: a whole-lake experiment on the Canadian Shield. *Ecosystems* 1: 120–136.
- Findlay, C. S., D. G. Bert & L. Zheng, 2000. Effect of introduced piscivores on native minnow communities in Adirondak lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 570–580.
- Hairton, N. G. & N. G. Hairston, 1993. Cause-effect relationships in energy-flow, trophic structure, and interspecific interactions. *The American Naturalist* 142: 379–411.
- Hairton, N. G. & N. G. Hairston, 1997. Does food web complexity eliminate trophic-level dynamics? *The American Naturalist* 149: 1001–1007.
- Hall, D. J., W. E. Cooper & E. E. Werner, 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography* 15: 839–929.
- Hambright, K. D., 1994. Morphological constraints in the piscivore–planktivore interaction: implications for the trophic cascade hypothesis. *Limnology and Oceanography* 39: 897–912.
- Hambright, K. D., R. J. Trebatoski, R. W. Drenner & D. Kettle, 1986. Experimental study of the impacts of bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) on pond community structure. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1171–1176.
- Hambright, K. D., R. W. Drenner, S. R. McComas & N. G. Hairston, 1991. Gape-limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. *Archiv für Hydrobiologie* 121: 389–404.
- Haney, J. F. & D. J. Hall, 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. *Limnology and Oceanography* 18: 331–333.
- Hanson, M. A. & M. G. Butler, 1990. Early responses of plankton and turbidity to biomanipulation in a shallow prairie lake. *Hydrobiologia* 200/201: 317–327.
- Hanson, M. A. & M. G. Butler, 1994a. Responses of plankton, turbidity and macrophytes to biomanipulation in a shallow prairie lake. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1180–1188.
- Hanson, M. A. & M. G. Butler, 1994b. Responses to food web manipulation in a shallow waterfowl lake. *Hydrobiologia* 279/280: 457–466.
- Havens, K. E., 1993. Responses to experimental fish manipulations in a shallow, hypereutrophic lake – the relative importance of benthic nutrient recycling and trophic cascade. *Hydrobiologia* 254: 73–80.
- Hoyle, J. A. & A. Keast, 1987. Prey handling time in two piscivores, *Esox americanus vermiculatus* and *Micropterus salmoides*, with contrasting mouth morphologies. *Canadian Journal of Zoology* 65: 540–542.
- Hoyle, J. A. & A. Keast, 1988. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Canadian Journal of Zoology* 66: 1972–1977.
- Hrbáček, J., D. Dvorakova, V. Korinek & L. Prochazkova, 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen* 14: 192–195.
- Hurlbert, S. H., 1997. Functional importance vs. keystone: reformulating some questions in theoretical biocenology. *Australian Journal of Ecology* 22: 369–382.

- Hurlbert, S. H. & M. S. Mulla, 1981. Impacts of mosquitofish (*Gambusia affinis*) predation on plankton communities. *Hydrobiologia* 83: 125–151.
- Hurlbert, S. H., J. Zedler & D. Fairbanks, 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. *Science* 175: 639–641.
- Jenkins, R. M., 1975. Black bass crops and species associations in reservoirs. In Stroud, R. H. & H. Clepper (eds), *Black bass Biology and Management*. Sport Fishing Institute, Washington DC, 114–124.
- Johnson, J.M. & D. M. Post, 1996. Morphological constraints on intracohort cannibalism in age-0 largemouth bass. *Transactions of the American Fisheries Society* 125: 809–812.
- Jeppesen, E., J. P. Jensen, M. Søndergaard & T. Lauridsen, 1997. Top-down control of freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* 342/343: 151–164.
- Jeppesen, E., J. P. Jensen, C. Jensen, B. Faafeng, D. O. Hessen, M. Søndergaard, T. Lauridsen, P. Brettum & K. Christoffersen, 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: a study of 466 lakes from the temperate to the arctic. *Ecosystems* 6: 313–325.
- Kalf, J., 2002. *Limnology: Inland Water Ecosystems*. Prentice Hall, New Jersey.
- Lamarra, V. A., 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen* 19: 2461–2468.
- Lancaster, H. F. & R. W. Drenner, 1990. Experimental mesocosm study on the separate and interaction effects of phosphorus and mosquitofish (*Gambusia affinis*) on plankton community structure. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 471–479.
- Mazumder, A., 1994a. Patterns of algal biomass in dominant odd-versus even-link lake ecosystems. *Ecology* 75: 1141–1149.
- Mazumder, A., 1994b. Phosphorus–chlorophyll relationships under contrasting herbivory and thermal stratification: predictions and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 390–400.
- Mazumder, A., 1994c. Phosphorus–chlorophyll relationships under contrasting zooplankton community structure: potential mechanisms. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 401–407.
- McQueen, D. J., 1998. Freshwater food web biomanipulation: a powerful tool for water quality improvement, but maintenance is required. *Lakes and Reservoirs: Research and Management* 3: 83–94.
- McQueen, D. J., J. R. Post & E. L. Mills, 1986. Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1571–1581.
- McQueen, D. J., C. W. Ramcharan & N. D. Yan, 2001. The Dorset food web piscivore manipulation project – Part 12: summary and emergent properties. *Archiv für Hydrobiologie Special Issues Advances in Limnology* 56: 257–288.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarette & S. B. Yamada, 1994. The keystone concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64: 249–286.
- Menzel, D. W. & N. Corwin, 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnology and Oceanography* 10: 280–282.
- Meijer, M.-L., E. H. R. R. Lammens, A. J. P. Raat, M. P. Grimm & S. H. Hosper, 1990. Impact of cyprinids on zooplankton and algae in ten drainable ponds. *Hydrobiologia* 191: 275–284.
- Miranda, L. E., 1983. Average ichthyomass in Texas large impoundments. *Proceedings of the Texas Chapter of the American Fisheries Society* 6: 58–67.
- Mittelbach, G. G. & L. Persson, 1998. The ontogeny of piscivory and its ecological implications. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1454–1465.
- Mittelbach, G. G., A. M. Turner, D. J. Hall & J. E. Rettig, 1995. Perturbation and resilience: a long-term, whole-lake study of predator extinction and reintroduction. *Ecology* 76: 2347–2360.
- Nowlin, W. H. & R. W. Drenner, 2000. Context-dependent effects of bluegill in experimental mesocosm communities. *Oecologia* 122: 421–426.
- Pace, M. L., J. J. Cole, S. R. Carpenter & J. F. Kitchell, 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14: 483–488.
- Page, L. M. & B. M. Burr, 1991. *The Peterson's Field Guide Series: A Field Guide to Freshwater Fishes*. Houghton Mifflin, New York.
- Polis, G. A. & D. R. Strong, 1996. Food web complexity and community dynamics. *The American Naturalist* 147: 813–846.
- Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong & J. Maron, 2000. When is a trophic cascade a trophic cascade?. *Trends in Ecology and Evolution* 15: 473–475.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. D. Daily, J. C. Castilla, J. Lubchenco & R. T. Paine, 1996. Challenges in the quest for keystones. *BioScience* 46: 609–620.
- Qin, J. & S. T. Threlkeld, 1990. Experimental comparison of the effects of benthivorous fish and planktivorous fish on plankton community structure. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie* 119: 121–141.
- Reynolds, C. S., 1994. The ecological basis for the successful biomanipulation of aquatic communities. *Archiv für Hydrobiologie* 130: 1–33.
- Richardson, W. B., S. A. Wickham & S. T. Threlkeld, 1990. Food-web response to the experimental manipulation of benthivore (*Cyprinus carpio*), zooplanktivore (*Menidia beryllina*) and benthic insects. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie* 119: 143–165.
- Schaus, M. H., M. J. Vanni, T. E. Wissing, M. T. Bremigan, J. E. Garvey & R. E. Stein, 1997. Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnology and Oceanography* 42: 1386–1397.
- Schaus, M. H., M. J. Vanni & T. E. Wissing, 2002. Biomass-dependent diet shifts in omnivorous gizzard shad: implications for growth, food web and ecosystem effects. *Transactions of the American Fisheries Society* 131: 40–54.
- Schindler, D. E., J. R. Hodgson & J. F. Kitchell, 1997. Density-dependent changes in individual foraging specialization of largemouth bass. *Oecologia* 110: 592–600.

- Schmitz, O. J., P. A. Hambach & A. P. Beckerman, 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removal on plants. *The American Naturalist* 155: 141–153.
- Shapiro, J., 1990. Biomanipulation: the next phase – making it stable. *Hydrobiologia* 200/201: 13–27.
- Shapiro, J. & D. I. Wright, 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. *Freshwater Biology* 14: 371–383.
- Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper & B. S. Halpern, 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5: 785–791.
- Spencer, C. N. & D. L. King, 1984. Role of fish in regulation of plant and animal communities in eutrophic ponds. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1851–1855.
- Stein, R. A., D. R. DeVries & M. M. Dettmers, 1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2518–2526.
- Tátrai, I., G. Tóth, J. E. Panyi, J. Zlinskzy & V. Istvánovics, 1990. Bottom-up effects of bream (*Abramis brama* L.) in Lake Balaton. *Hydrobiologia* 200/201: 167–175.
- Tátrai, I., J. Oláh, G. Paulovits, K. Mátyás, B. J. Kawiecka, V. Jozsa & F. Pekár, 1997. Biomass dependent interactions in pond ecosystems: responses of lower trophic levels to fish manipulations. *Hydrobiologia* 345: 117–129.
- Tonn, W. M. & C. A. Paszkowski, 1986. Size-limited predation, winterkill, and the organization of *Umbra-Perca* fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 194–202.
- Tonn, W. M., C. A. Paszkowski & I. J. Holopainen, 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. *Ecology* 73: 951–958.
- Tremmel, B., K. H. Nicholls, D. J. McQueen, C. W. Ramcharan & A. Pérez-Fuentetaja, 2001. Did phytoplankton biovolume and taxonomic composition change? In DeMott, W. R. (ed.), *The Dorset food web piscivore manipulation project*. *Archiv für Hydrobiologie – Advances in Limnology* #56, Stuttgart, .
- Turner, A. M. & G. G. Mittelbach, 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* 71: 2241–2254.
- Van Veldhoven, P. P. & G. P. Mannaerts, 1987. Inorganic and organic phosphate measurements in the nanomolar range. *Analytical Biochemistry* 161: 45–48.
- Wagner, K. J., 1986. Biological management of a pond ecosystem to meet water use objectives. In Redfield, G., J. F. Taggart & L. M. Moore (eds), *Lake and Reservoir Management Volume II – Proceedings of the 5th Annual Conference and International Symposium of the North American Lake Management Society*, 1985, Geneva, Wisconsin. North American Lake Management Society, Washington DC, 54–59.
- Welcomme R., L., 1988. *A History of International Introductions of Inland Aquatic Species*. United Nations Food and Agricultural Organization, Fisheries Technical Paper Number 294, Rome.
- Werner, E. E. & D. J. Hall, 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69: 1352–1366.
- Wetzel, R. G., 1983. *Limnology* (2nd edn.) Harcourt Brace Publishers, New York.
- Wilkinson, L., 1998. *SYSTAT 8.0 User's Manual, Version 8.0*. SYSTAT Inc, Evanston, Illinois.
- Wood, L. W., 1985. Chloroform–methanol extraction of chlorophyll. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 38–43.