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ASSESSING THE TROPHIC CASCADE IN RESERVOIRS:
THE ROLE OF AN INTRODUCED PREDATOR

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

John M. Dettmers, B.S., M.S.

******

The Ohio State University
1995

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CHAPTER I
INTRODUCTION

Food web dynamics in aquatic systems commonly are approximated by linear energy transfer among trophic levels (Oksanen et al. 1981; Persson et al. 1992). Implications of these interactions on community structure have been explored in a variety of systems, including north temperate lakes (Shapiro and Wright 1984; Vanni et al. 1990a; Kitchell 1992; Carpenter and Kitchell 1993; McQueen et al. 1992; Persson et al. 1992), streams (Power 1990), and marine intertidal zones (Paine 1980). Whereas food web effects have been documented to propagate linearly, researchers have disagreed about whether energy inputs most likely alter trophic levels above or below that level initially affected (DeMelo et al. 1992; Carpenter and Kitchell 1992).

Because top-down interaction strength varies with nutrient availability, trophic interactions are neither exclusively top-down nor bottom-up, but some combination of each (McQueen et al. 1986; Hunter and Price 1992). Nutrients do strongly influence phytoplankton abundance; however, their effects on higher trophic levels appear unclear (McQueen et al. 1986; Mazumder 1994). In turn,
piscivores most often strongly influence trophic interactions down to zooplankton (McQueen et al. 1989), but their effects on phytoplankton are less clear (DeMelo et al. 1992). In oligotrophic waters, piscivore effects likely cascade down to phytoplankton (Carpenter et al. 1987; McQueen 1990), whereas more eutrophic lakes appear less likely to exhibit top-down effects on phytoplankton (McQueen et al. 1986). These findings illustrate that top-down and bottom-up forces work in concert to structure food webs.

Whereas this suite of trophic interactions appears common and tightly regulated in natural, northern hemisphere lakes, these interactions likely are less tightly linked in systems that have developed in the absence of coevolution (e.g., Great Lakes and reservoir communities). Of particular management concern is the potential for decoupling predator-prey dynamics, which may result in weak trophic linkages (Stewart et al. 1981; Stein et al. in press). In reservoirs, forage fishes, especially shad *Dorosoma* spp., can be extremely abundant in the presence of native piscivores (Summers and Axon 1979; Filipek 1980; Orth 1980; Willis and Jones 1986). In fact, gizzard shad *D. cepedianum* are preferred prey (Johnson et al. 1988, Wahl and Stein 1988), but at most 30% of gizzard shad production is consumed by piscivores in Ohio reservoirs (Carline et al. 1984, Johnson et al. 1988).
By virtue of its abundance, gizzard shad exerts strong top-down effects on zooplankton, especially during early life stages (DeVries and Stein 1992; Dettmers and Stein 1992). As an omnivore >30 mm TL, gizzard shad can eliminate zooplankton, then switch to phytoplankton and detritus (Miller 1960; Bodola 1966), thus persisting in reservoirs at quite high densities. By eliminating zooplankton, gizzard shad may compromise recruitment of planktivorous sport fishes (e.g., bluegill *Lepomis macrochirus*), and may reduce survival of young-of-year largemouth bass (*Micropterus salmoides*) through indirect effects (DeVries et al. 1991; Stein et al. in press).

Because gizzard shad may structure reservoir communities (DeVries and Stein 1992; Stein et al. in press), control of gizzard shad becomes important to resource managers as they seek to improve sport fishing opportunities and water quality. Hence, I sought to understand how reservoir food webs function while simultaneously determining whether managers could use piscivores to improve sport-fish recruitment and water clarity. My dissertation research employed ecological experiments at multiple scales coupled with bioenergetics modeling to 1) examine the generality of the trophic cascade hypothesis as it applies to reservoirs and 2) generate management insight into appropriate strategies for controlling gizzard shad in Ohio reservoirs.
Chapter II employs both short-term laboratory experiments and quantification of gizzard shad diets in reservoirs to determine the potential for omnivorous gizzard shad to consume more zooplankton if more was available in the environment. The laboratory experiment demonstrated the potential for gizzard shad to consume more zooplankton if more was available. The field portion of this work verified this result and documented how gizzard shad size and zooplankton availability altered laboratory patterns.

In Chapter III, I explore the functioning of reservoir food webs. I first reviewed the literature to assess the potential of several piscivores to reduce shad populations. I then used a pond experiment to quantify the top-down responses of age-0 gizzard shad, zooplankton, and phytoplankton to hybrid striped bass.

I more specifically evaluated the relative importance of top-down and bottom-up processes in permitting zooplankton persistence in Chapter IV. Here, I used sets of in-reservoir enclosures, distributed across three reservoirs, reflecting a gradient of zooplankton production that mimicked the range of zooplankton production across all Ohio reservoirs. To each set of enclosures, I added four densities of gizzard shad to determine zooplankton persistence both as a function of gizzard shad food consumption and zooplankton production.
In Chapter V, I combined laboratory size-selection experiments and bioenergetics modeling to predict the impact of hybrid striped bass on gizzard shad. Size-selection experiments illustrated patterns of hybrid striped bass consumption. Bioenergetics modeling predicted whether hybrid striped bass could reduce gizzard shad and permit increased zooplankton abundance, assuming several levels of gizzard shad consumption, gizzard shad mortality, and hybrid striped bass stocking rates.

These experiments provide insight into how reservoir food webs are structured. By understanding the suite of basic ecological interactions that occur in reservoir food webs, I generated useful insight into how frequently I might expect top-down interactions to improve sport-fish recruitment and water clarity and hence the relative usefulness of stocking piscivores to modify reservoir food webs.
CHAPTER II

EXPLORING POTENTIAL REGULATION OF SUMMER ZOOPLANKTON

BY OMNIVOROUS GIZZARD SHAD

Introduction

Predators can structure aquatic communities (Carpenter and Kitchell 1993); planktivorous fishes alter zooplankton species composition (Brooks and Dodson 1965; Prophet 1982, 1988), size structure (Brooks and Dodson 1965; DeVries and Stein 1992; Lazzaro et al. 1992), and abundance (Guest et al. 1990; Bremigan et al. 1991; Dettmers and Stein 1992). Impacts on zooplankton communities fluctuate as fish grow because many fish undergo ontogenetic shifts in food use (Werner and Gilliam 1984). These shifts may derive, in part, from changes in prey abundance (Wu and Culver 1992). Complex interactions between ontogenetic feeding shifts and seasonal prey fluctuations likely cause fishes to modify their diet.

Gizzard shad *Dorosoma cepedianum* often dominate fish communities in reservoirs (Jenkins 1967; Cramer and Marzolf 1970; Noble 1981; Johnson et al. 1988) and may regulate summer zooplankton. As larvae < 30 mm TL, gizzard shad consume zooplankton almost exclusively (Bodola 1966; Cramer
and Marzolf 1970; DeVries et al. 1991; Dettmers and Stein 1992), reducing zooplankton to low levels (< 20 \text{L}^{-1}) (Bremigan et al. 1991; DeVries and Stein 1992). By reducing zooplankton, gizzard shad exacerbates exploitative competition among reservoir fishes dependent on limited zooplankton (e.g., bluegill Lepomis macrochirus), perhaps compromising recruitment of these fishes (Guest et al. 1990; DeVries et al. 1991; Dettmers and Stein 1992; Stein et al., in press).

Beyond 30 mm TL, gizzard shad become filter feeders consuming not only zooplankton, but also detritus (Bodola 1966; Cramer and Marzolf 1970; Drenner et al. 1982b). In laboratory experiments, gizzard shad 57-189 mm TL effectively filter zooplankton (Drenner et al. 1982a, 1982b). By contrast, field evidence reveals that gizzard shad > 38 mm TL consume primarily detritus (Mundahl 1988, 1991; Mundahl and Wissing 1987, 1988).

Gizzard shad may regulate reservoir communities from their position in the middle of the food web because they eliminate zooplankton, but remain abundant by feeding on detritus and by being invulnerable to predators due to fast first-year growth (Stein et al., in press). In my view, gizzard shad > 30 mm are opportunistic foragers consuming zooplankton when it is abundant, feeding on detritus when zooplankton declines, and switching back to zooplankton as zooplankton increases. To test this hypothesis, I completed
feeding trials with different amounts of zooplankton and detritus, and then compared these results to gizzard shad diets in reservoirs.

Methods

Laboratory Experiments

Gizzard shad were collected via electrofishing from Kokosing and Knox lakes (Knox County, Ohio) during March and April 1992, and maintained in the laboratory with Artemia nauplii. Detritus was collected from the littoral zone of Kokosing Lake in March 1992, whereas zooplankton was obtained from ponds at the Hebron State Fish Hatchery (Licking County, Ohio) during March and April 1992.

I established four treatments: 1) high zooplankton (100 zooplankters·L⁻¹) only (ZPO; N=5 replicates), 2) high zooplankton and detritus (HZPD; N=5), 3) low zooplankton (20 zooplankters·L⁻¹) and detritus (LZPD; N=5), and 4) detritus only (DO; N=3). HZPD reflects minimum zooplankton densities (100·L⁻¹) required for sport fish recruitment (Eldridge et al. 1981; Li and Mathias 1982; Werner and Blaxter 1980) and matched densities in Clark Lake. LZPD was chosen because gizzard shad frequently drive zooplankton below 20·L⁻¹ in reservoirs (DeVries et al. 1991; Dettmers and Stein 1992; DeVries and Stein 1992) and matched densities in Kokosing Lake.

Detritus (3-5 cm) was added to 114-L aquaria 4 d before experiments began, whereas zooplankton was added 24 h before
experiments. Two gizzard shad, starved for 24 h, were placed in each aquarium for 1 h, then removed, measured (nearest mm), and frozen for analysis later. Two gizzard shad were used per aquarium so as to enhance feeding. During experiments, I characterized feeding behavior every 5 min for 1 min by noting foraging position, either scooping bottom detritus or filter-feeding zooplankton from the water column.

To quantify diet, I removed both pharyngeal pockets, the foregut, and the gizzard. I examined gut contents with a dissecting microscope and measured all intact zooplankters (nearest 0.001 mm) and converted length to biomass (Dumont et al. 1975; Bottrell et al. 1976; Culver et al. 1985). Gut contents were dried for 24 h at 60° C. Zooplankton weight in each gut was calculated by summing individual zooplankton weights. Detritus weight was calculated as the difference between calculated zooplankton weight and gut-contents weight.

Gizzard shad wet weights were calculated as per Johnson et al. (1988):

\[
\ln (W) = 3.357 \cdot \ln (L) + (-12.97)
\]

\(W\) = wet body weight

\(L\) = total length.

I analyzed overall treatment effects via one-way analysis of variance (ANOVA) and employed Tukey's multiple comparisons to examine treatment differences.
Field Pattern

Study Lakes. Kokosing Lake was a 65-ha reservoir with 7.5 km of shoreline, a mean depth of 2.0 m (maximum depth = 4.9 m), and Secchi depths typically < 100 cm. Neither submersed nor emergent vegetation was abundant. Clark Lake (Clark County, Ohio) was a 40-ha reservoir with 4.5 km of shoreline, a mean depth of <1.0 m (maximum depth = 2.0 m), and typical Secchi depths varied from 25 to 75 cm. Emergent vegetation (*Typha* spp.) occupied about 25% of the shoreline. Fish communities in both lakes included gizzard shad, largemouth bass *Micropterus salmoides*, white crappie *Pomoxis annularis*, bluegill *Lepomis macrochirus*, and common carp *Cyprinus carpio*.

Collection and Analysis. I collected juvenile gizzard shad via electrofishing or seining from Kokosing Lake on six dates during June through November and from Clark Lake on seven dates during July through August 1992. Fish were immediately placed on ice. Gut contents of 7-15 fish collected from each date and lake were quantified as described above.

Simultaneous with seine samples, zooplankton samples (16-33 L per sample, N=3 per date) were collected using a tube sampler (2 m long, 72 mm diameter). Each sample was then filtered through a 54-μm mesh net, preserved in 70% ethyl alcohol, and counted as per Stahl and Stein (1994). Up to 20 individuals of each taxon in a sample were measured
(nearest 0.01 mm), allowing me to calculate biomass via
taxon-specific, length-dry weight regressions (Dumont et al.
1975; Bottrell et al. 1976; Culver et al. 1985).

I evaluated weight-specific zooplankton consumption by
young-of-year gizzard shad using regression analysis. Data
were log-transformed to satisfy normality assumptions.

Results

Laboratory Experiments

Mean total lengths of gizzard shad in experiments were
ZPO (N = 10), 101.60 ± 5.36 mm (mean ± 1 SE), HZPD (N = 10),
105.00 ± 5.18 mm, LZPD (N = 10), 103.30 ± 2.40 mm, and DO (N
= 6), 74.17 ± 1.99 mm. Gizzard shad in the detritus only
treatment were smaller than fish in the other treatments
(ANOVA: F = 8.142, df = 3,32, P = 0.0001; Tukey’s multiple
comparisons, P < 0.05); hence, all comparisons among
treatments were evaluated as mg of zooplankton or detritus
consumed per g wet body weight of gizzard shad.

Gizzard shad scooped bottom detritus. This foraging
activity often suspended detritus in the water column,
leading to occasional detrital filter feeding by gizzard
shad. With abundant zooplankton, gizzard shad filter-fed in
the water column.

Crustacean zooplankton stocked into aquaria were
dominated by Bosmina, but also contained nauplii and
copepods. Gizzard shad consumed zooplankton in all
treatments with zooplankton. Zooplankton biomass consumed
differed among treatments (ANOVA: $F = 4.129$, $df = 3,32$, $P = 0.014$; Figure 1a). Gizzard shad in the ZPO and HZPD treatments consumed similar amounts of zooplankton but more zooplankton than gizzard shad in the LZPD treatment (Tukey's multiple comparisons, $P = 0.089$; Figure 1). Gizzard shad in the ZPO treatment consumed primarily zooplankton. Gizzard shad in the HZPD consumed equal proportions of zooplankton and detritus by weight, whereas gizzard shad in the LZPD and DO treatments primarily consumed detritus. In the ZPO treatment, carapaces and algae from guts were considered detritus because they had fallen to the bottom, where gizzard shad fed on them as if they were detritus. I maintained zooplankton with algae and did not remove carapaces from the tanks between trials; hence, carapaces and algae occurred in all treatments. Detritus consumed did not differ among treatments (ANOVA: $F = 1.289$, $df = 3,32$, $P = 0.295$). The proportion of detritus in gizzard shad guts varied from 0.19 in the ZPO treatment to 1.00 in the DO treatment (Figure 1).

**Field Pattern**

Mean total lengths of gizzard shad from Clark ($N = 87$) and Kokosing ($N = 62$) lakes were $52.6 \pm 1.9$ mm (mean $\pm$ SE) and $51.8 \pm 11.7$ mm, respectively. Gizzard shad collected via electrofishing were generally larger than those collected via seining.
Mean crustacean zooplankton biomass differed between lakes (t-test: \( P = 0.0001 \)). Clark Lake zooplankton density and biomass persisted at high levels during 2 July-9 September, maintaining density at \( 64-158 \cdot L^{-1} \) and biomass at \( 90-196 \mu g \cdot L^{-1} \). Kokosing Lake zooplankton density and biomass remained low during 25 June-9 September, declining to zero on 15 July and never increasing above \( 25 \cdot L^{-1} \) and \( 27 \mu g \cdot L^{-1} \), respectively.

Gizzard shad from Kokosing and Clark lakes primarily consumed detritus (Figure 2). Weight-specific detritus consumption did not differ between lakes (paired \( t \)-test: \( P = 0.88 \)). No other trends in detritus consumption were evident, either between lakes or across fish size. Gizzard shad always consumed > 97% detritus (Figure 2).

Weight-specific zooplankton consumption declined as gizzard shad grew from 30-60 mm in both reservoirs (Figure 2). Gizzard shad 60-100 mm then maintained constant, low zooplankton consumption, resulting in a negative correlation between weight-specific zooplankton consumption and gizzard shad size (Table 1; Figure 2). Zooplankton consumption by gizzard shad tended to increase when more zooplankton were available in Clark Lake, but not in Kokosing Lake (Table 1; Figure 3). To assess the combined influence of gizzard shad size and zooplankton availability on zooplankton consumption, I used multiple regression. In this analysis, only gizzard shad size was a significant predictor when
modeled with zooplankton biomass (Table 1; Figure 4). In addition, the interaction term was not significant. Thus, the effects of gizzard shad size and zooplankton availability on zooplankton consumption did not shift with changes in the other variable. Despite zooplankton consumption declining with size, this decline did not affect the capacity of gizzard shad to consume more zooplankton if more became available. However, the stronger determinant of overall gizzard shad consumption was gizzard shad size.

Discussion

With laboratory and field data, I have described feeding by gizzard shad juveniles 30-100 mm. Laboratory and field data were congruent regarding weight-specific zooplankton consumption by juvenile gizzard shad when exposed to both zooplankton and detritus. When zooplankton biomass exceeded 90 μg·L⁻¹ (HZPD treatment and Clark Lake), gizzard shad 60-100 mm consumed 1-3 μg zooplankton·g⁻¹ fish, whereas when zooplankton biomass fell below 27 μg·L⁻¹ (LZPD treatment and Kokosing Lake), gizzard shad 60-100 mm ate 0.1-0.3 μg zooplankton·g⁻¹ fish. In Kokosing Lake, gizzard shad consumption was unrelated to zooplankton availability because so little was available (< 30 μg·L⁻¹), as compared to Clark Lake (90-200 μg·L⁻¹). Interestingly, zooplankton consumption by juvenile gizzard shad declined by an order of magnitude as zooplankton biomass declined by 70% from Clark to Kokosing lake.
Though laboratory and field data revealed similar patterns of consumption, these patterns have different origins. Laboratory data were collected from aquaria for 1 h at constant temperature whereas field data represent a point estimate in guts of gizzard shad subject to variable feeding times and temperatures. Despite this variability, feeding patterns in field and laboratory closely mimicked one another; thus, size-dependent processes drove foraging patterns, not environmental conditions.

In the field, weight-specific zooplankton consumption by juvenile gizzard shad declined 1-3 orders of magnitude as gizzard shad grew from 30 to 60 mm. Beyond 60 mm, weight-specific zooplankton consumption by gizzard shad remained constant. Thus, juvenile gizzard shad 1) ate less zooplankton as they grew and 2) ate more zooplankton if more zooplankton biomass became available, even after their switch to omnivory.

This dietary pattern of gizzard shad is consistent with the literature. Larval gizzard shad consume only crustacean zooplankton (Dettmers and Stein 1992; DeVries and Stein 1992). Juvenile and adult gizzard shad consume zooplankton, phytoplankton, and detritus (Miller 1960; Bodola 1966), frequently feeding primarily on detritus (Mundahl 1988). During growth from larval to adult life stages, gizzard shad ingest zooplankton to provide critical protein because this
diet item often limits detritivore growth (Bowen et al. 1995).

Despite eating primarily detritus after growing > 60 mm, juvenile gizzard shad can exert strong top-down effects on zooplankton simply because of increasing overall consumption by juvenile gizzard shad (Dettmers and Stein 1992), coupled with generally low zooplankton productivity during summer. Even though gizzard shad consume few zooplankton, this consumption may be sufficient to maintain low zooplankton density when productivity is low.

At low summer zooplankton densities, gizzard shad likely do not vary their zooplankton consumption (e.g., Kokosing Lake). Gizzard shad < 60 mm may strongly influence summer zooplankton in Kokosing Lake because they consume substantial amounts of zooplankton, whereas larger gizzard shad do not. However, gizzard shad 60-100 mm can increase their zooplankton consumption as zooplankton biomass increases (e.g., Clark Lake). These large gizzard shad, if abundant, likely regulate summer zooplankton dynamics in productive reservoirs.

These complex interactions among gizzard shad feeding ontogeny and zooplankton biomass provide useful insight into how gizzard shad, through several life stages, can influence reservoir zooplankton and determine recruitment success of planktivorous sport fishes. Because gizzard shad likely regulate reservoir communities from a position in the middle
of the food web, their effects on zooplankton travel up as well as down the food web (Stein et al., in press). I believe juvenile gizzard shad 30-60 mm maintain low summer zooplankton levels in reservoirs. If predators can reduce these juveniles such that zooplankton remains > 100·L⁻¹ (Dettmers et al., in press), then recruitment of planktivorous sport fishes (e.g., bluegill *Lepomis macrochirus*) could be improved. However, if large gizzard shad invulnerable to predators simply incorporate the resulting zooplankton into their diet, then gizzard shad circumvent the top-down impact of predators and maintain an environment unsuitable for early, zooplanktivorous life stages of sport fishes.
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to fry density. Canadian Journal of Fisheries and Aquatic Sciences 37:1063-1069.


Table 1. Regressions predicting the weight-specific amount of zooplankton present in YOY gizzard shad guts (µg·g⁻¹) during June-September 1992 in Clark Lake and during June-November 1992 in Kokosing Lake, as a function of a) gizzard shad size, b) zooplankton biomass, and c) both gizzard shad size and zooplankton biomass. The equation takes the form of: log(zooplankton in gut) = a + b[log(response)]. ZP = zooplankton biomass available in each lake.

<table>
<thead>
<tr>
<th>Equation</th>
<th>N</th>
<th>r²</th>
<th>P</th>
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<tbody>
<tr>
<td><strong>Clark Lake</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a) 4.12 - 0.04*(size)</td>
<td>25</td>
<td>0.53</td>
<td>0.000 1</td>
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<tr>
<td>b) 0.60 + 0.01*(ZP)</td>
<td>5</td>
<td>0.58</td>
<td>0.14</td>
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<tr>
<td>c) 12.2 - 2.71*(size) + 0.03*(ZP)</td>
<td>17</td>
<td>0.59</td>
<td>0.002</td>
</tr>
<tr>
<td><strong>Kokosing Lake</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a) 4.72 - 0.08*(size)</td>
<td>17</td>
<td>0.39</td>
<td>0.01</td>
</tr>
<tr>
<td>b) 1.50 - 0.02*(ZP)</td>
<td>6</td>
<td>0.02</td>
<td>0.77</td>
</tr>
<tr>
<td>c) 13.64 - 3.12*(size) - 0.35*(ZP)</td>
<td>17</td>
<td>0.49</td>
<td>0.01</td>
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</table>
Figure 1. Mean crustacean zooplankton dry biomass (± 1 SE) consumed per gram wet body weight of gizzard shad (left y-axis; solid circles) and mean percent detritus in gizzard shad guts (right y-axis; open circles) during experiments in 114-L aquaria. I used 10 replicate fish in each aquarium treatment, except for DO, where only 6 were used. ZPO = zooplankton only; HZPD = high zooplankton plus detritus; LZPD = low zooplankton plus detritus; DO = detritus only. The line in the upper left portion of panel A signifies similar zooplankton consumption, as determined by Tukey's multiple comparisons (P > 0.05).
Figure 1

Proportion Detritus

Detritus
Zooplankton

ug Zooplankton, g fish^{-1}

0 4 8 12 16

0.94 0.96 0.98 1.00

ZPO  HZPD  LZPD  DO
(e.g., Clark Lake) (e.g., Kokosing Lake)

Figure 1
Figure 2. Mean crustacean zooplankton dry biomass (± 1 SE) consumed per gram wet body weight of gizzard shad (left y-axis) and mean percent detritus in gizzard shad guts (right y-axis), as for 10-mm size classes in Clark (A) and Kokosing (B) lakes, Ohio, during June-November, 1992. Numbers in parentheses reflect sample sizes for each size class.
Figure 2

A. Clark Lake

B. Kokosing Lake

Gizzard Shad Length Classes (mm TL)

Field Lab

Detritus

Zooplankton

Proportion Detritus

ug Zooplankton·g fish⁻¹
Figure 3. Mean crustacean zooplankton dry biomass consumed per gram wet body weight of gizzard shad (log(x + 1) transformed) as a function of zooplankton dry biomass available (μg·L⁻¹) in Clark (A) and Kokosing (B) lakes, Ohio during June through November, 1992. Note differences in X-axis scales between panels, reflecting the nearly 10x greater zooplankton biomass in Clark Lake.
A. Clark Lake

\[ Y = 0.6 + 0.01X \]

N = 5

\[ r^2 = 0.58 \]

p = 0.14

B. Kokosing Lake

Figure 3
Figure 4. Response curve of mean crustacean zooplankton biomass consumed per gram wet body weight of gizzard shad versus lakewide zooplankton biomass available and gizzard shad size class in Clark (A) and Kokosing (B) lakes, Ohio, during June-November, 1992. Note differences in Y- and Z-axis scales between lakes.
A. Clark Lake

B. Kokosing Lake

Figure 4
CHAPTER III
RESERVOIR BIOMANIPULATION: QUANTIFYING PISCIVORE EFFECTS AND PREY PRODUCTIVITY ACROSS MULTIPLE TROPHIC LEVELS

Introduction

The trophic cascade hypothesis provides an intuitive understanding of top-down effects of fishes on lower trophic levels, given existing nutrient levels (Carpenter et al. 1985; Carpenter et al. 1987; McQueen et al. 1989; Carpenter and Kitchell 1993). These trophic interactions are common at the piscivore-planktivore, planktivore-zooplankton, and zooplankton-phytoplankton levels (DeMelo et al. 1992) in natural lakes because planktivores most often consume zooplankton, and large zooplankton grazers (i.e., Daphnia spp.) are abundant. As a result, the trophic cascade hypothesis also can be applied (i.e., biomanipulation) to reduce abundant populations of planktivorous fishes (Stewart et al. 1981) or to improve water clarity in north temperate lakes (Carpenter et al. 1985; Shapiro and Wright 1984; Benndorf 1990; Kitchell 1992).

In reservoirs, resident piscivores frequently do not control the abundance of prey fishes, especially gizzard shad *Dorosoma cepedianum* because it exhibits high fecundity
(Vondracek and LeHew 1991), rapid growth, and limited vulnerability to piscivores (Adams and DeAngelis 1987; Johnson et al. 1988b; Hambright et al. 1991; Stein et al., in press). Simultaneously, gizzard shad imposes its own control on lower trophic levels, eliminating crustacean zooplankton populations (Drenner et al. 1982a,b; Dettmers and Stein 1992; DeVries and Stein 1992). However, age-0 gizzard shad are not resource limited by zooplankton because they can successfully consume phytoplankton and detritus (Miller 1960; Bodola 1966).

Omnivorous gizzard shad thrive in reservoirs (Summers and Axon 1979), persisting at high densities even after early summer zooplankton populations decline. By exploitative competition for limited zooplankton in early summer, age-0 gizzard shad can reduce growth, survival, and abundance of other age-0 fishes (Guest et al. 1990; DeVries et al. 1991). Further, large reductions in zooplankton abundance do not translate to increased phytoplankton in reservoir enclosures, unless Daphnia spp. occur at densities > 40·L⁻¹ (Dettmers and Stein, in press). Thus, trophic interactions in reservoirs containing gizzard shad appear weakly linked owing to 1) omnivory and fast growth by gizzard shad (making it invulnerable to resource depletion and piscivores) and 2) absence of large-bodied herbivorous zooplankton. Consequently, gizzard shad may regulate reservoir communities from its position in the middle of the
food web, by affecting trophic levels above and below it (Stein et al., in press).

Even given this bleak outlook for biomanipulation, resource managers seek to improve sport fishing opportunities in reservoirs by reducing gizzard shad (Crandall 1978; Ott and Malvestuto 1981; Jahn et al. 1987; DeVries and Stein 1990). Introducing large-gaped, fast-growing piscivores that strongly overlap with gizzard shad in the open water could reduce gizzard shad abundance sufficiently to release zooplankton from predation, thereby improving opportunities for enhanced recruitment of sport fishes and increased herbivory by zooplankton. Herein, I first investigate, via a literature review, the potential for piscivores to generate top-down effects in reservoirs. I then experimentally evaluate the potential for successful biomanipulation in reservoirs by evaluating the top-down impact of hybrid striped bass *Morone saxatilis* x *M. chrysops* on zooplankton and phytoplankton in ponds dominated by age-0 gizzard shad.

**Methods**

**Literature review.**--Resident piscivores, though exerting top-down effects in natural lakes, do not exert strong control of gizzard shad in reservoirs (see Results). Because *Morone* predators are frequently stocked to consume shad (Pritchard et al. 1976), I reviewed the literature to determine how introduced *Morone* predators influence shad,
zooplankton, and phytoplankton. For each study assessed, I noted species (i.e., striped bass *M. saxatilis*, white bass *M. chrysopt*, or hybrid striped bass; gizzard shad, threadfin shad *Dorosoma petenense*), stocking conditions, site characteristics, author's conclusions regarding shad control, and the evidence supporting their conclusions.

**Pond experiment.**—This experiment was conducted at the Hebron State Fish Hatchery, located near Buckeye Lake in Licking County, Ohio. Eight ponds (0.4 ha, mean depth=1 m) were filled with water from a canal connected to Buckeye Lake; water was filtered through a 245-μm microstrainer to eliminate any larval fishes but permit colonization by zooplankton and phytoplankton. At each pond, inflow water was strained through a 500-μm mesh Saran sock as an added precaution. Ponds required about 7 d to fill, after which a constant, low inflow of water replaced evaporation and leakage across dikes.

I added 40 adult gizzard shad (about 5 kg·ha⁻¹) in spawning condition to each pond on May 7, 1993 such that I could expect abundant age-0 gizzard shad without confounding the experiment with extensive adult effects. Hybrid striped bass (*N*=59 per pond; 184-400 mm) were added to four randomly chosen ponds on May 28, at an initial density of 22 kg·ha⁻¹. On that same day, I added 45 kg·ha⁻¹ common carp *Cyprinus carpio* (> 250 mm TL) to all ponds to increase turbidity and thus more closely mimic reservoir conditions. I sampled
age-0 gizzard shad, crustacean zooplankton, and phytoplankton weekly during May 13-July 15, 1993 to assess their responses to my piscivore manipulation. Gizzard shad were sampled May 13-June 23 with an ichthyoplankton net (0.5-m diameter, 500-μm mesh) towed at about 1.0 m·s⁻¹ at the surface of each pond. Total larval production during May 13-June 23 was estimated by summing pond-wide larval abundance estimates across sampling dates. After June 9, I collected gizzard shad by shoreline seining with a 10-m long, 6.25-mm mesh seine, sampling three 10-m transects per pond. Zooplankton and phytoplankton were collected with an integrated tube sampler (72 mm inside diameter) that sampled the entire water column (DeVries and Stein 1991). Zooplankton were filtered through a 54-μm mesh net and preserved in 4% sucrose formalin (Haney and Hall 1973). Hybrid striped bass diets and diel food consumption were quantified on June 17 and June 30. Trap nets were checked every 3 h over 24 h in two ponds. I weighed and measured all hybrid striped bass caught. Stomach contents were recovered by pulsed gastric lavage and frozen.

During July 19-21, 1993, I drained all ponds, collected remaining fish, and placed them in raceways, where I quantified biomass and size distribution. All hybrid striped bass were individually weighed (nearest g) and measured (nearest mm); stomach contents were recovered as described above to quantify piscivore size selection. I
determined size distributions of other fishes (gizzard shad, carp, and bluegill *Lepomis macrochirus*) by individually weighing and measuring all fish (at least 50 age-0 gizzard shad per pond) collected in a haphazardly selected sample (range: 965-2500 g) from each pond. All remaining fish were sorted by species and weighed. Bluegill were incidentally introduced into three ponds when I added carp on May 28. Age-0 bluegill did not appear in ponds until July 7 and never contributed > 2% of age-0 fish biomass.

Only crustacean zooplankton were counted in the laboratory (Stahl and Stein 1994); hence, in the remaining text I use the term zooplankton to refer to crustacean zooplankton. Up to 20 individuals of each taxon in a sample were measured (nearest 0.01 mm) on a digitizing tablet viewed through a microscope drawing tube. These measurements provided size distributions and allowed me to calculate biomass via taxon-specific, length-dry weight regressions (Dumont et al. 1975; Bottrell et al. 1976).

Phytoplankton were concentrated by filtering water through a 0.45-µm filter, placed on a cover slip, and cleared with 2-hydroxypropyl methacrylate. Cover slips were then dried for 12 h, mounted to a slide (N=3 slides per sample), and counted using a compound microscope with Nomarski optics at 200x and 400x. At least 15 fields were counted at each magnification to achieve a coefficient of variation of < 10% (St. Amand 1990). Edible algae were
defined as diatoms, chrysophytes, and chlorophytes < 35 μm in the greatest axial linear dimension (GALD). Inedible algae included these taxa that were > 35 μm GALD, as well as all cyanophytes and dinoflagellates.

I calculated crustacean zooplankton production (dry weight) as the increase in mass of existing individuals plus the number of eggs produced each week (Culver and DeMott 1978). I used temperature-dependent growth and egg development equations to determine the time zooplankters spent in each stage (DeMott 1976; Bean 1980). Zooplankton growth plus fecundity provided taxon-specific production estimates. These estimates were then summed across taxa to generate estimates of total zooplankton production for each weekly interval.

I saved up to 20 age-0 gizzard shad from shoreline seining in each pond on each sampling date to quantify diets. Age-0 gizzard shad diets (N=5 fish per pond per date) were examined by excising the pharyngeal pockets, esophagus, foregut, and gizzard. I counted and measured all zooplankton consumed and calculated biomass consumed using taxon-specific, length-dry weight regressions (see above).

Hybrid striped bass fish prey were measured (total, standard, or backbone length, depending on stage of digestion) and identified to species; partially digested prey were identified via structures resistant to digestion.
I back-calculated prey weight at ingestion using length-weight relationships (Wahl and Stein 1991).

I analyzed treatment effects for age-0 gizzard shad abundance, total zooplankton density, size, biomass, production, and phytoplankton biovolume using split-plot repeated-measures analysis of variance (Maceina et al. 1994). Treatment effects were compared from the last sampling date prior to piscivore addition (May 26), until I ended the experiment (July 15). When necessary, data were normalized with a log(x+1) transformation.

Results

Literature Review.

The impact of piscivores on lower trophic levels has been well-documented in natural lakes (DeMelo et al. 1992). Piscivores that have exerted strong top-down impacts in natural lakes, e.g., largemouth bass *Micropterus salmoides* (Carpenter et al. 1987; Hall and Ehlinger 1989), northern pike *Esox lucius* (McQueen et al. 1989), and walleye *Stizostedion vitreum vitreum* (Johnson et al. 1992), cannot regulate gizzard shad populations in reservoirs, despite their preference for gizzard shad (Carline et al. 1984; Johnson et al. 1988a; Wahl and Stein 1991). In fact, I found no evidence in the peer-reviewed literature of successful reduction of shad abundance by black basses, percids, or esocids. In one example, typical largemouth bass size distributions permit about 30% of gizzard shad to
be invulnerable to predation due to gape limitation (Hambright et al. 1991). Failure of resident piscivores to control shad has prompted managers to begin stocking *Morone* spp. in attempts to reduce gizzard shad abundance (Pritchard et al. 1976). Here I consider the evidence for success, relative to gizzard shad reduction, of *Morone* introductions; unfortunately, no work to date has explored the response of zooplankton or phytoplankton to these piscivores.

I compiled 69 papers that dealt with 190 *Morone* introductions. Shad populations were monitored in 26 introductions, of which 15 dealt with introduction of striped bass, 9 with hybrid striped bass, 1 with both striped bass and hybrid striped bass, and 1 with white bass (Table 2). Of the 26 introductions, only 7 included any pre-*Morone* data and just 1 included any statistical treatment. For these introductions, 15 concluded that some form of shad control occurred, 7 concluded shad were not controlled, and 4 studies did not explicitly link changes in shad populations to *Morone* introduction (Table 2). The perception of authors, though not rigorously documented, is that *Morone* control shad under some circumstances. Of the 15 studies concluding that some form of shad control occurred, 6 cited reduced abundance, 1 cited changes in shad size, 5 cited changes in both, and 3 concluded that shad were controlled, yet did not discuss any response parameters (Table 2).
Given the perceived relative success of Morone introductions at controlling gizzard shad abundance (15 of 26 introductions), I chose to use Morone piscivores in my experiment because no other piscivores have been introduced with the intent to reduce gizzard shad (DeVries and Stein 1990). Hence, I believed that Morone was an appropriate candidate to generate top-down effects that could conceivably cascade to zooplankton and phytoplankton. Hybrid striped bass were used because warm Ohio reservoirs would compromise summer survival of striped bass.

**Pond experiment.**

Larval gizzard shad abundance peaked at 25 $\cdot$ m$^{-3}$ in ponds to be stocked with hybrid striped bass and at 9 $\cdot$ m$^{-3}$ in ponds that were to remain piscivore-free on May 13 (Figure 5). Before Morone introduction, larval abundance did not differ between treatments on any given day (Figure 5) or across the entire larval sampling period (repeated measures ANOVA; $F=3.99$; df 1,3; $P=0.14$). Similarly, larval gizzard shad production in ponds with hybrid striped bass did not differ from piscivore-free ponds (t-test; $P=0.18$), despite multiple spawning by gizzard shad that occurred only in the piscivore treatment. I infer multiple gizzard shad spawning events in ponds containing hybrid striped bass given the late larval peak on June 16 (Figure 5) and reduced larval gizzard shad size, relative to piscivore-free ponds at this time (Figure 6b).
Hybrid striped bass did not consume age-0 gizzard shad < 25 mm. On June 17, when larval gizzard shad occurred at 8·m⁻³, hybrid striped bass (N=7) ate 61 prey, only one of which was a fish. Similarly, on June 30, hybrid striped bass (N=5) ate 15 prey, but only one fish. I could not estimate the size for either of these fish prey due to advanced digestion. At draining, when 76% of hybrid striped bass diets (N=91 guts) by weight consisted of fish, mean length of gizzard shad eaten (N=78; mean length=39.5 mm) was smaller than the mean length of age-0 gizzard shad (N=318; mean length=57.4 mm) in ponds (t-test; df=394; P<0.0001).

Hybrid striped bass reduced age-0 gizzard shad abundance relative to piscivore-free ponds, as measured by shoreline seining (Table 3; Figure 6a), but did not reduce common carp abundance (repeated measures ANOVA, P=0.87). This treatment effect resulted from the greater abundance of age-0 gizzard shad in piscivore-free ponds on June 9 and 16 (Figure 6a). The significant time x treatment interaction resulted from the steep age-0 gizzard shad decline in piscivore-free ponds (Table 3; Figure 6a). Gizzard shad abundance declined to near zero in piscivore-free ponds after June 29 (Figure 6a), when the weight-specific amount of zooplankton in their guts declined below that of gizzard shad in ponds with hybrid striped bass (t-test on each date; df=4; P<0.04). Further, gizzard shad length declined in ponds with piscivores (Table 3; Figure 6b), despite fewer gizzard shad in these ponds. A
marginally significant time x treatment interaction occurred because gizzard shad length in piscivore-free ponds increased during June 9-July 15, whereas mean gizzard shad length in ponds with hybrid striped bass never exceeded 30 mm (Table 3; Figure 6b). However, at the end of the experiment there was no treatment effect on gizzard shad length (t-test; p=0.20), biomass (t-test; p=0.40) or abundance (t-test; p=0.43). In turn, hybrid striped bass did not influence either common carp or bluegill length (t-tests; p>0.52), biomass (t-tests; p>0.67), or abundance (t-tests; p>0.65) at the end of the experiment.

Zooplankton abundance was similar between treatments before hybrid striped bass addition but was greater in ponds with hybrid striped bass after piscivore addition (Table 3; Figure 7a). Zooplankton density was higher with piscivores on June 10, June 16, and July 6, but not on the remaining dates (Figure 7a). The time x treatment interaction resulted from zooplankton being nearly eliminated by gizzard shad in piscivore-free ponds, and then subsequently rebounding after gizzard shad abundance declined (Table 3; Figure 7a). However, the overall response of zooplankton production was only marginally greater in ponds with hybrid striped bass (Table 3; Figure 7c), despite greater zooplankton production on each individual date during June 10-July 6 (Figure 7c). Zooplankton size increased with hybrid striped bass (Table 3; Figure 7b), primarily because
zooplankton were larger during June 23-July 6 in ponds with piscivores. Zooplankton size did decline in piscivore-free ponds after June 29, resulting in a significant time x treatment interaction (Table 3; Figure 7b). Top-down effects of hybrid striped bass did allow larger zooplankton to remain more abundant (at levels > 100·L⁻¹ during June and July) than in ponds without piscivores, but only beginning four weeks after piscivore addition.

Neither total phytoplankton biovolume nor the inedible fraction responded to piscivore addition (Table 3). The overall response of edible phytoplankton biovolume was marginally greater in piscivore-free ponds (Table 3; Figure 7d), due to increased edible phytoplankton in ponds without hybrid striped bass on June 23. No time or time x treatment effects were significant in any of my phytoplankton analyses.

Mean zooplankton density in ponds during June 2-July 15 was negatively related to peak age-0 gizzard shad density, as estimated by shoreline seining, and positively related to mean zooplankton production during June 2-July 15 (Figure 8). Age-0 gizzard shad density and zooplankton production explained 97% of the observed variation in mean zooplankton density across all ponds (Table 4). Further, this experiment illustrates the impact of piscivores, driving age-0 gizzard shad abundance to sufficiently low levels to permit zooplankton persistence. Incorporating phytoplankton
main effect and interaction terms into this model provided no additional explanatory power to the observed pattern of zooplankton abundance.

I then compared this model with a relationship developed from 1-m³ in-reservoir enclosures that predicted zooplankton persist at > 100·L⁻¹ only if age-0 gizzard shad density is < 10·m⁻³ and zooplankton production exceeds 220 mg·m⁻³·d⁻¹ dry weight (Dettmers and Stein, in press). The pond relationship mimicked that from enclosures (test for differences between regression lines; $F=0.17; \text{df } 3,40; P=0.92$), providing strong, independent confirmation of the processes by which age-0 gizzard shad abundance and zooplankton productivity determine zooplankton density (Figure 9). Hybrid striped bass reduced gizzard shad, permitting mean zooplankton density to increase in piscivore ponds relative to piscivore-free ponds. I conclude that zooplankton persist only if age-0 gizzard shad density remains below 10·m⁻³ and zooplankton production exceeds 220 mg·m⁻³·d⁻¹ dry weight in the presence of hybrid striped bass.

Discussion

Few resident piscivores are likely to reduce gizzard shad abundance in reservoirs, due to diet diversity and gape limitation (Saiki and Ziebell 1976; Hambright et al. 1991). My literature review revealed that authors perceived that *Morone* predators commonly reduced shad abundance. However, authors almost universally failed to apply appropriate
statistical evaluation or to use adequate experimental design to validate these perceptions (sensu DeVries and Stein 1990). Thus, these literature data suggest, but are insufficient to allow me to conclude, that Morone can control shad populations.

The literature review also suggested that system productivity was consistently considered an important influence on the ability of Morone to control shad. For example, declining threadfin shad abundance in Lake Mead, AZ-NV was attributed to a combination of striped bass predation and declining phytoplankton abundance (due to reduced nutrient availability after completion of an upstream dam; Persons and Dreyer 1987). In Lake Powell UT-AZ, increased striped bass abundance led to dramatic reductions in shad abundance, which were previously thought to be limited by resource availability in this oligotrophic system (Gustaveson et al. 1984, 1990). In fact, the only factor believed to have allowed threadfin shad to persist despite increased predation was the presence of turbid refuges in canyons and bays (Gustaveson et al. 1984).

My pond experiment demonstrated that hybrid striped bass reduced age-0 gizzard shad, permitting zooplankton to persist at > 100·L\(^{-1}\) during June 2-July 15. However, increased zooplankton abundance, size, and production was not sufficient to reduce edible phytoplankton biovolume. Thus, hybrid striped bass can reduce age-0 gizzard shad and
permit zooplankton to persist, at least in systems with high zooplankton productivity.

With piscivores, age-0 gizzard shad size increased slowly because hybrid striped bass likely eliminated the largest individuals as they grew to a size that was vulnerable to these piscivores early in the experiment. In ponds with hybrid striped bass, mean age-0 gizzard shad size exceeded 25 mm only after July 7, whereas age-0 gizzard shad mean size in piscivore-free ponds was nearly 25 mm by June 8 (a full month earlier). However, the dry weight to wet weight ratio for age-0 gizzard shad was greater in ponds with hybrid striped bass during June 9-June 29, reflecting greater food availability. However, age-0 gizzard shad grew well after June 29 because, despite low zooplankton abundance, this resource was less limiting due to reduced gizzard shad abundance. Age-0 gizzard shad grew well in ponds with piscivores, but mean age-0 gizzard shad size remained low due to size-selective predation by hybrid striped bass. Despite likely selecting large age-0 gizzard shad early in the experiment, hybrid striped bass selected small age-0 gizzard shad at the end of the experiment, given gizzard shad growth patterns.

When age-0 gizzard shad are abundant and grow > 25 mm, their consumptive demand rapidly increases (Dettmers and Stein 1992), resulting in reduced zooplankton. Age-0 gizzard shad likely depleted zooplankton in piscivore-free
ponds because they grew beyond 25 mm by early June. Whereas weight-specific zooplankton consumption by individual age-0 gizzard shad was greater in piscivore ponds after June 29, population consumption was lower owing to lower densities and smaller size in the presence of hybrid striped bass (as compared to piscivore-free ponds).

Whereas reducing age-0 gizzard shad population, consumption is necessary for abundant zooplankton to persist, this condition is not sufficient. In 1-m³ enclosures, even when age-0 gizzard shad occurred at < 10 fish·m⁻³, zooplankton could be eliminated if zooplankton production was low (Dettmers and Stein, in press). Zooplankton persisted in enclosures only when two conditions were fulfilled: 1) when age-0 gizzard shad density was < 10·m⁻³ and 2) when zooplankton production exceeded 220 mg·m⁻³·d⁻¹. In my pond experiment, mean zooplankton production after June 1 was 257 mg·m⁻³·d⁻¹ dry weight in ponds with hybrid striped bass, but only 54 mg·m⁻³·d⁻¹ dry weight in piscivore-free ponds, explaining why zooplankton persisted only in my piscivore treatment and providing support for the perception generated by the literature review that system productivity influences the potential for gizzard shad control.

Despite strong top-down zooplankton responses, edible phytoplankton biovolume was unaffected, a result consistent with results from north temperate lakes without abundant
large zooplankton (Carpenter et al. 1985) and my 1-m$^3$ enclosure results, where zooplankton could only influence phytoplankton when Daphnia spp. were > 40·L$^{-1}$ (Dettmers and Stein, in press). In piscivore ponds, Daphnia spp. density never exceeded 39·L$^{-1}$ after June 1. In addition, resuspension of nutrients by carp may have permitted increased algal biomass, masking potential zooplankton effects (Havens 1993). Consequently, I suggest that phytoplankton did not respond because few Daphnia spp. occurred in my ponds and because of potential nutrient resuspension by carp.

Management Implications

My results reveal that zooplankton abundance can be sustained under high zooplankton productivity coupled with low age-0 gizzard shad abundance maintained by hybrid striped bass. The potential for piscivores to increase zooplankton abundance depends both on zooplankton productivity and age-0 gizzard shad density (Dettmers and Stein, in press). In turn, the success of piscivore manipulations, relative to improved sport fish recruitment, likely will depend on the density of zooplankton permitted to persist.

At least 100 zooplankters·L$^{-1}$ are required for reasonable recruitment of larval fishes (Eldridge et al. 1981; Li and Mathias 1982; Werner and Blaxter 1980). Thus, improved bluegill and crappie Pomoxis spp. recruitment may occur if
piscivores sufficiently reduce age-0 gizzard shad abundance, especially if other planktivores are rare. Such improved recruitment may not be realized if hybrid striped bass consume these sport-fish prey. However, hybrid striped bass survived poorly in small (< 50 ha) Oklahoma reservoirs containing only bluegill (Layzer and Clady 1981). In a Texas reservoir containing 2-20x greater bluegill biomass than shad species, hybrid striped bass diets still consisted of 50-90% shad and 10-20% bluegill by volume (Crandall 1978). Thus, hybrid striped bass likely will exert only minimal predation on spiny-rayed sport fishes.

Piscivores may influence the position of individual reservoirs on the response surface by consuming age-0 gizzard shad. Hybrid striped bass shifted age-0 gizzard shad density to the left on the response surface, permitting zooplankton abundance to increase. Effective age-0 gizzard shad predators may permit a greater peak density of age-0 gizzard shad to coexist with abundant zooplankton because piscivores quickly reduce age-0 gizzard shad as they grow > 25 mm and intensively consume zooplankton. For instance, in my experiment, ponds without hybrid striped bass exhibited a mean peak age-0 gizzard shad (> 25 mm) density of 11.3·m⁻³, above the minimum threshold for biomanipulation, whereas age-0 gizzard shad density in ponds with piscivores peaked at only 1.7·m⁻³.
Extrapolating my results to reservoirs, managers must consider age-0 gizzard shad density, zooplankton productivity, and potential age-0 gizzard shad consumption by piscivores. Without considering these factors simultaneously, managers are unlikely to predict those reservoirs suitable for top-down responses. For instance, in 44% (21 of 48) of Ohio reservoir-years, age-0 gizzard shad abundance was below $10 \cdot m^3$ (Bremigan et al. 1991; DeVries et al. 1991; DeVries and Stein 1992; N. S. Donovan, Aquatic Ecology Laboratory, unpublished data). Of 21 reservoir-years, only 3 (14%) exceeded my zooplankton production threshold of $220 \text{ mg} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ (Dettmers and Stein in press; JMD, M. T. Bremigan, Aquatic Ecology Laboratory, unpublished data). Both age-0 gizzard shad density and zooplankton production criteria must be met within a single reservoir for successful biomanipulation. Assuming these criteria to be independent, I multiply probabilities to predict that about 6% of Ohio reservoirs have age-0 gizzard shad abundance $< 10 \cdot m^3$ coupled with zooplankton production $> 220 \text{ mg} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$ to permit zooplankton densities $> 100 \cdot \text{L}^{-1}$.

Because hybrid striped bass can reduce age-0 gizzard shad abundance by about $10 \cdot m^3$, this piscivore has the potential to improve sport-fish recruitment in reservoirs with up to 20 age-0 gizzard shad $\cdot m^{-3}$ and high zooplankton productivity. Under this relaxed gizzard shad criterion, 11% of Ohio reservoirs may be amenable to biomanipulation.
However, my piscivore effects occurred in small ponds, potentially reducing their impact in larger reservoirs due to the presence of other available prey fishes.

Additionally, age-0 gizzard shad 30-100 mm eat primarily detritus but can consume more zooplankton if more is available (L. A. Yako, Aquatic Ecology Laboratory, unpublished data). Hence, when age-0 gizzard shad are reduced (as in my ponds), I believe larger gizzard shad may incorporate the additional zooplankton into their diet and, if they are abundant, circumvent the top-down impact of hybrid striped bass. Thus, hybrid striped bass likely will not generate zooplankton densities $> 100 \cdot \text{L}^{-1}$ in all reservoirs containing $< 20$ age-0 gizzard shad $\cdot \text{m}^{-3}$ and high zooplankton productivity.

Top-down effects of hybrid striped bass reduced age-0 gizzard shad abundance and increased zooplankton, but did not cascade to phytoplankton. Improved reservoir water clarity is unlikely through piscivore-induced responses given the small size of zooplankton across most Ohio reservoirs (Bremigan et al. 1991; Aquatic Ecology Laboratory, unpublished data). However, biomanipulation may occur in reservoirs when zooplankton densities are $> 100 \cdot \text{L}^{-1}$ if piscivores maintain age-0 gizzard shad abundance below $10 \cdot \text{m}^{-3}$ and zooplankton production exceeds $220 \text{ mg} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$. Fewer than 11% of Ohio reservoirs are suitable for biomanipulation in this context; hence, the potential for
increasing zooplankton abundance to improve sport fish recruitment by reducing age-0 gizzard shad is a limited option for reservoir managers.
Literature Cited


Dettmers, J. M., and R. A. Stein. In press. Quantifying linkages among gizzard shad, zooplankton, and
phytoplankton in reservoirs. Transactions of the American Fisheries Society.


Hanson, J. A. 1980. Evaluation of programs designed to reduce adverse interactions between fingerling largemouth bass and threadfin shad. California Department of Fish and Game, Final Performance Report, Project F-34-R, Sacramento.

Harper, J. L. 1982. Striped bass research study-population trends (Texoma Reservoir). Oklahoma Department of


Jester, D. B. and B. L. Jensen. 1972. Life history and ecology of the gizzard shad, Dorosoma cepedianum (LeSueur) with reference to Elephant Butte Lake. New Mexico State University, Agricultural Experimental Station, Research Report 218.


Table 2. Summary of published studies that quantified response of shad (*Dorosoma* spp.) populations to *Morone* spp. introduction. Studies were grouped by predator species and perceived success of shad control. Abundance (abnd) and size frequency under author's conclusion relate to abundance and size of shad populations.

<table>
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<tr>
<th>Lake</th>
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<th>Species*</th>
<th>Stocking density (fish/ha)</th>
<th>Pre-*Morone data?</th>
<th>Statistical treatment of data?</th>
<th>Authors conclude control?</th>
<th>Reference(s)</th>
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<td>Smith Mountain Lake, VA</td>
<td>8,337</td>
<td>SB/GS</td>
<td>up to 97.1 mean=36.5 fing</td>
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<td>NA</td>
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<td>Ney et al. 1988</td>
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<td></td>
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<td>Moore et al. 1985</td>
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<td>6.6x10⁶</td>
<td>SB/TS</td>
<td>0.0098 fish</td>
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<td>No</td>
<td>Yes-abnd</td>
<td>Persons and Dreyer 1987</td>
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<td>SB/TS</td>
<td>0.3-3.5 fing.</td>
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<td>No</td>
<td>Yes-abnd</td>
<td>Gustaveson et al. 1984, 1990</td>
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<td>684</td>
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<td>5.0-7.5 fing., adult</td>
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<td>No</td>
<td>Yes-no data</td>
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<td>SB/GS+TS</td>
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<tr>
<td>Location</td>
<td>Population</td>
<td>Growth Stage</td>
<td>Life History</td>
<td>Reproduction</td>
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<td>Herrington Lake, KY</td>
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<td>Yes</td>
<td>No</td>
<td>Morris and Follis 1978</td>
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<td>72 fing.</td>
<td>Yes</td>
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<td></td>
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<td>Nash et al. 1987</td>
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<td>1,692</td>
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<td>D'Arbonne Lake, LA</td>
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<td>SB/?</td>
<td>723,000 fing. over 13 yrs</td>
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<td>No</td>
<td>Od</td>
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<td>Toledo Bend Res., LA</td>
<td>72,640</td>
<td>SB/?</td>
<td>2,642,000 fing. over 13 yrs</td>
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<td>20-30</td>
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<td>No</td>
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<td>Douglas 1986; Jahn et al. 1987</td>
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<td></td>
<td></td>
<td>19-79 mm</td>
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<td>No</td>
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<td>367</td>
<td>25 fish</td>
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<td>40</td>
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<td>214 fry</td>
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<td>No/Yes*</td>
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<td>10,121</td>
<td>84-150 fry+fing.</td>
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<td>19.4-58.9 fing.</td>
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<td></td>
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<td>No</td>
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<td></td>
<td></td>
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<td>fry+fing.</td>
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<td>No</td>
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<th>Abundance</th>
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<td></td>
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<td>Elephant Butte Lk., NM</td>
<td>16,327</td>
<td>WB/GS</td>
<td>?</td>
<td>No</td>
<td>No</td>
<td>Yes-abnd and size</td>
</tr>
</tbody>
</table>

* SB=striped bass, HSB=hybrid striped bass, WB=white bass, GS=gizzard shad,
  TS=threadfin shad

b fing=Morone stocked as fingerlings
c gizzard shad size shifted, but this could not be attributed to Morone
d No conclusions drawn
e pre-Morone data in Kleinholz and Maughan 1984, but not in Muoneke et al. 1987
  statistics used in Muoneke et al. 1987 but not in Kleinholz and Maughan 1984.
Table 3. Summary of split-plot repeated measures ANOVA results for the various response variables to the hybrid striped bass treatment in 0.4-ha ponds at the Hebron State Fish Hatchery, Ohio, during May 26-July 15, 1993. The column labelled change refers to the direction of the response by each variable to the hybrid striped bass treatment and time main effects. NA refers to the Time x Treatment interaction term, which cannot be classified by simple directional summary. Note that I tested for differences in zooplankton density before and after hybrid striped bass were added to ponds, whereas I tested for differences in age-0 gizzard shad density, age-0 gizzard shad length, zooplankton size, zooplankton production (dry weight), edible phytoplankton biovolume, and inedible phytoplankton biovolume only after hybrid striped bass were added to ponds.

<table>
<thead>
<tr>
<th>Response</th>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gizzard shad density</td>
<td>Treatment</td>
<td>1</td>
<td>1185770.11</td>
<td>33.67</td>
<td>0.01</td>
<td>↓</td>
</tr>
<tr>
<td></td>
<td>Time</td>
<td>5</td>
<td>547197.91</td>
<td>12.67</td>
<td>0.0001</td>
<td>↓</td>
</tr>
<tr>
<td></td>
<td>Time x Treatment</td>
<td>5</td>
<td>595219.40</td>
<td>13.78</td>
<td>0.0001</td>
<td>NA</td>
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Table 3 (continued),

Gizzard shad length

<table>
<thead>
<tr>
<th></th>
<th>Treatment</th>
<th>1</th>
<th>782.02</th>
<th>24.24</th>
<th>0.02</th>
<th>↓</th>
</tr>
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<tbody>
<tr>
<td>Time</td>
<td></td>
<td>5</td>
<td>519.43</td>
<td>18.35</td>
<td>0.0001</td>
<td>↑</td>
</tr>
<tr>
<td>Time x Treatment</td>
<td></td>
<td>5</td>
<td>68.72</td>
<td>2.43</td>
<td>0.06</td>
<td>NA</td>
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ln(zooplankton density)

<table>
<thead>
<tr>
<th></th>
<th>Treatment</th>
<th>1</th>
<th>0.02</th>
<th>0.00</th>
<th>0.95</th>
<th>↔</th>
</tr>
</thead>
<tbody>
<tr>
<td>during May 13 - May 26</td>
<td>Time</td>
<td>2</td>
<td>4.23</td>
<td>5.36</td>
<td>0.02</td>
<td>↑</td>
</tr>
<tr>
<td>(pre-treatment)</td>
<td>Time x Treatment</td>
<td>2</td>
<td>0.88</td>
<td>1.12</td>
<td>0.36</td>
<td>NA</td>
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</table>

ln(zooplankton density)

<table>
<thead>
<tr>
<th></th>
<th>Treatment</th>
<th>1</th>
<th>21.74</th>
<th>24.98</th>
<th>0.02</th>
<th>↑</th>
</tr>
</thead>
<tbody>
<tr>
<td>during June 2 - July 15</td>
<td>Time</td>
<td>6</td>
<td>2.59</td>
<td>6.32</td>
<td>0.0001</td>
<td>↓</td>
</tr>
<tr>
<td>(post-treatment)</td>
<td>Time x Treatment</td>
<td>6</td>
<td>2.01</td>
<td>4.91</td>
<td>0.001</td>
<td>NA</td>
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</tbody>
</table>
Table 3 (continued),

<table>
<thead>
<tr>
<th>Treatment</th>
<th>ln(zooplankton size)</th>
<th>ln(zooplankton production)</th>
<th>Total phytoplankton biovolume</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>40.60</td>
<td>5.69 x 10^{18}</td>
</tr>
<tr>
<td>Time</td>
<td>7</td>
<td>15.28</td>
<td>2.68 x 10^{19}</td>
</tr>
<tr>
<td>Time x Treatment</td>
<td>7</td>
<td>1.39</td>
<td>1.39</td>
</tr>
</tbody>
</table>

|                           |                      |                             |                               |
|                           | Treatment            |                             |                               |
|                           | 1                    | 1.13                        | 8.44                          |
|                           |                      |                             |                               |
|                           | Time                 | 0.87                        | 0.86                          |
|                           |                      |                             |                               |
|                           | Time x Treatment     | 0.25                        | 0.25                          |
|                           |                      |                             |                               |
|                           | 40.60                | 13.15                       | 0.96                          |
|                           |                      |                             |                               |
|                           | 15.28                | 13.15                       | 0.96                          |
|                           |                      |                             |                               |
|                           | 1.39                 | 1.19                        | 0.96                          |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           | Treatment            |                             |                               |
|                           | 1                    | 1.13                        | 8.44                          |
|                           |                      |                             |                               |
|                           | Time                 | 0.87                        | 0.86                          |
|                           |                      |                             |                               |
|                           | Time x Treatment     | 0.25                        | 0.25                          |
|                           |                      |                             |                               |
|                           | 40.60                | 13.15                       | 0.96                          |
|                           |                      |                             |                               |
|                           | 15.28                | 13.15                       | 0.96                          |
|                           |                      |                             |                               |
|                           | 1.39                 | 1.19                        | 0.96                          |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
|                           |                      |                             |                               |
Table 3 (continued),

<table>
<thead>
<tr>
<th></th>
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<th>Time</th>
<th>Treatment</th>
<th>Time</th>
<th>Treatment</th>
<th>Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Edible phytoplankton biovolume</td>
<td>1</td>
<td>8.38 x 10^{11}</td>
<td>6.13</td>
<td>0.09</td>
<td>↔</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>2.07 x 10^{12}</td>
<td>10.40</td>
<td>0.0001</td>
<td>↓</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>2.47 x 10^{11}</td>
<td>1.24</td>
<td>0.31</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>Inedible phytoplankton biovolume</td>
<td>1</td>
<td>1.14 x 10^{19}</td>
<td>1.33</td>
<td>0.33</td>
<td>↔</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>8.92 x 10^{18}</td>
<td>0.95</td>
<td>0.47</td>
<td>↔</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>8.93 x 10^{18}</td>
<td>0.95</td>
<td>0.47</td>
<td>NA</td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Regression equations predicting zooplankton density in 0.4-ha ponds, with and without the hybrid striped bass main effect, and the regression summarizing all experiments in enclosures (Dettmers and Stein in press) and ponds (current study). In all cases the dependent variable is log(zooplankton density). Symbols are: GS=peak age-0 gizzard shad density, as measured by shoreline seining; ZPRD=mean zooplankton production (dry weight) during June 2-July 15, 1993; HSB=indicator variable for presence or absence of hybrid striped bass; TYPE=indicator variable describing pond or enclosure experiment.

<table>
<thead>
<tr>
<th>Equation</th>
<th>$r^2$</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ponds, without hybrid striped bass main effect</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$3.43 - 0.30\times\log(GS) + 0.41\times\log(ZPRD)$</td>
<td>0.97</td>
<td>111.69</td>
<td>0.0001</td>
</tr>
<tr>
<td><strong>Ponds, with hybrid striped bass main effect</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$3.60 - 0.54\times\log(GS) + 0.53\times\log(ZPRD) + 0.54\times(HSB)$</td>
<td>0.99</td>
<td>250.10</td>
<td>0.0001</td>
</tr>
<tr>
<td><strong>Enclosures and ponds</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$-0.75 + 0.12\times\log(GS) + 0.86\times\log(ZPRD) + 1.11\times(TYPE)$</td>
<td>0.89</td>
<td>111.62</td>
<td>0.0001</td>
</tr>
</tbody>
</table>
Figure 5. Mean (± 1 SE) larval gizzard shad (< 25 mm TL) density collected with a 0.5-m diameter, 500-μm mesh ichthyoplankton net in 0.4-ha ponds at the Hebron State Fish Hatchery, Ohio, during May 13–June 23, 1993. N=4 ponds per treatment. Hybrid striped bass were added to ponds on May 28, 1993. P-values represent results from t-tests on each date to determine whether larval gizzard shad density differed across treatments.
Larval Gizzard Shad Density (Number/m$^3$)

- No Hybrid Striped Bass
- Hybrid Striped Bass

Figure 5
Figure 6. Mean (± 1 SE) number of age-0 gizzard shad collected via shoreline seining (A) during June 9-July 15, 1993, and the mean total length of larval (< 25 mm TL) and juvenile gizzard shad (≥ 25 mm) in 0.4-ha ponds (B) at the Hebron State Fish Hatchery, Ohio, during May 13-July 15, 1993. N=4 ponds per treatment. Hybrid striped bass were added to ponds on May 28, 1993. In both panels, ponds containing hybrid striped bass are represented by solid symbols, whereas predator-free ponds are represented by open symbols. Asterisks denote significant treatment effects (*=P< 0.05).
Figure 6
Figure 7. Mean (± 1 SE) zooplankton density (A), zooplankton size (B), zooplankton production (C; dry weight), and edible phytoplankton biovolume (D) in 0.4-ha ponds at the Hebron State Fish Hatchery, Ohio, during May 13-July 15, 1993. N=4 ponds per treatment. Hybrid striped bass were added to ponds on May 28, 1993. Note that y-axis scales on all panels are arithmetic, except for panel C, which is logarithmic. Asterisks denote significant treatment effects (*=P<0.05; **=P<0.01; ***=P<0.001).
Figure 7
Figure 8. Plots of mean zooplankton density during June 2-July 15, 1993 as a function of peak age-0 gizzard shad abundance, as measured by shoreline seining (A), and mean zooplankton production (B; dry weight) during June 2-July 15, 1993 in 0.4-ha ponds at the Hebron State Fish Hatchery, Ohio.
Figure 8

**Figure 8A**

- Hybrid Striped Bass
- No Hybrid Striped Bass

**Figure 8B**

- Mean Zooplankton Density (Number L⁻¹)
- Mean Zooplankton Production (mg m⁻³ d⁻¹)

- $r^2 = 0.73$
- $p = 0.004$
Figure 9. Response surface of zooplankton remaining in 1-m³ enclosures after 28-d experiments, as functions of the number of age-0 gizzard shad retrieved from each enclosure and final zooplankton production (dry weight). Results derived from 0.4-ha ponds at the Hebron State Fish Hatchery during 1993 are plotted with the response surface. This surface was interpolated with a smoothing function using data from experiments in Clark, Kokosing, and Knox lakes, Ohio during 1991 and 1992 and has been presented in a form without the pond data in Dettmers and Stein (in press).
Figure 9
CHAPTER IV
QUANTIFYING LINKAGES AMONG GIZZARD SHAD, ZOOPLANKTON, AND PHYTOPLANKTON IN RESERVOIRS

Introduction

The trophic cascade hypothesis is a useful conceptual framework for investigating the processes governing community interactions in natural lakes (Kitchell and Carpenter 1993). This hypothesis provides an intuitive basis for understanding top-down effects of fishes on lower trophic levels at given nutrient levels (Carpenter et al. 1987; McQueen et al. 1989; Carpenter and Kitchell 1993). This framework also can provide insight into strategies for managing lake communities (Shapiro and Wright 1984; Benndorf 1990; Kitchell 1992).

Top-down trophic interactions are quite predictable at the piscivore-planktivore and planktivore-zooplankton levels but are more equivocal at the zooplankton-phytoplankton level (DeMelo et al. 1992). The unpredictable strength of top-down responses at the zooplankton-phytoplankton link may be due primarily to lake trophic status (McQueen et al. 1986), with more eutrophic lakes less likely to exhibit top-down effects unless large Daphnia spp. are abundant (Vanni
et al. 1990b; McQueen et al. 1992). However, rigorous experimental tests of the potential interaction between lake trophic state and planktivore density have revealed no influence on phytoplankton biomass (reviewed in Lancaster and Drenner 1990; DeMelo et al. 1992).

Trophic interactions in reservoirs depart from the strongly linked interactions common to northern lakes where native predators can control prey fish abundance and, in turn, modify lower trophic levels (Carpenter et al. 1987; Lyons 1987; McQueen et al. 1989). For example, in reservoirs, native predators frequently do not control the abundance of prey fishes, especially shad *Dorosoma* spp. (Summers and Axon 1979; Filipek 1980; Orth 1980; Willis and Jones 1986). Although gizzard shad *D. cepedianum* are preferred prey (Johnson et al. 1988; Wahl and Stein 1988), high fecundity (Vondracek and LeHew 1991), fast growth, and large adult size limit their vulnerability to predators (Adams and DeAngelis 1987; Johnson et al. 1988; Hambright et al. 1991; Stein et al., in press). In Ohio reservoirs, only 20% of gizzard shad production is consumed by predators (Carline et al. 1984; Johnson et al. 1988).

Further, gizzard shad impose their own control on lower trophic levels (Drenner et al. 1982a, b; Dettmers and Stein 1992; DeVries and Stein 1992), without being strongly regulated by zooplankton and phytoplankton abundance. Age-0 gizzard shad > 25 mm, when sufficiently abundant, can
virtually eliminate crustacean zooplankton in reservoirs (Dettmers and Stein 1992; DeVries and Stein 1992) and then switch to feeding on phytoplankton and detritus (Miller 1960; Bodola 1966). Thus, age-0 gizzard shad can reduce growth, survival, and abundance of other planktivorous age-0 fishes by exploitative competition for zooplankton (Guest et al. 1990; DeVries et al. 1991) while maintaining high population densities.

Gizzard shad > 100 mm feed primarily on detritus (Mundahl and Wissing 1988; Mundahl 1991). However, if abundant, this life stage also can regulate zooplankton and phytoplankton. In mesocosm experiments, adult gizzard shad increased primary productivity and reduced crustacean zooplankton abundance, effects which were stronger in more productive mesocosms (Drenner et al., in press). By feeding on detritus, gizzard shad may regulate zooplankton and phytoplankton by moving nutrients from sediments to the pelagia, where they can be used by phytoplankton (Vanni 1995). As a result, all life stages of gizzard shad may regulate reservoir communities via complex "middle-out" processes that affect both higher and lower trophic levels (Stein et al., in press).

Given their dramatic effects on food webs, gizzard shad reduction by large, nonresident predators may be an attractive option to resource managers who seek to improve sport fishing opportunities and water clarity by increasing
zooplankton abundance. These predators must consume sufficient gizzard shad to release zooplankton populations from planktivore control, thereby increasing recruitment potential of resident sport fishes and increasing grazing pressure on phytoplankton.

Here, I determine how several densities of age-0 gizzard shad influenced crustacean zooplankton abundance in reservoirs with different capacities for producing zooplankton. If zooplankton increases as gizzard shad abundance declines, I expect more zooplankton 1) to be available for early life stages of sport fishes and 2) to increase grazing pressure on phytoplankton.

Study Area

Clark Lake, in Clark County, west-central Ohio, is a 40-ha, shallow, turbid reservoir with 4.5 km of shoreline, a maximum depth of 2 m, and Secchi depths of 25-75 cm that supports high zooplankton productivity. Kokosing Lake, in Knox County, central Ohio, is a 65-ha, shallow reservoir with 7.5 km of shoreline, a maximum depth of 4.9 m, and Secchi depths of 40-110 cm that supports intermediate zooplankton productivity. Knox Lake, also in Knox County, is a 225-ha reservoir with 19.2 km of shoreline, a maximum depth of 9.6 m, and Secchi depths of 60-140 cm that supports low zooplankton productivity. Rooted vegetation was rare or nonexistent in all lakes. Fish communities consisted primarily of gizzard shad, largemouth bass *Micropterus*
salmoides, crappies Pomoxis spp., sunfishes Lepomis spp., yellow perch Perca flavescens, channel catfish Ictalurus punctatus, carp Cyprinus carpio, and bullhead Ameiurus spp. I chose these lakes because sampling in 1987-1991 (Bremigan et al. 1991; Dettmers and Stein 1992) revealed that their crustacean zooplankton production was representative of the range encountered in Ohio reservoirs.

**Methods**

I placed 12 floating enclosures (1.1 m diameter, 1 m deep, 1 m³ volume; excluding sediments) in Kokosing Lake on May 8, 1991, and 16 enclosures each in Clark Lake on May 12, 1992, and in Knox Lake on May 13, 1992. Enclosures were filled with lake water before larval fish occurred, permitting crustacean zooplankton assemblages to develop for about 5 weeks without fish predation. I sampled zooplankton and phytoplankton in each bag weekly in May-July with four pooled hauls of a tube sampler (7.2 cm inside diameter; DeVries and Stein 1991). Zooplankton were filtered through a 54-μm mesh net and preserved in 4% sucrose formalin (Haney and Hall 1973).

In all lakes, I randomly assigned enclosures to four treatment levels (Table 1). Gizzard shad treatment densities were chosen to increasingly challenge crustacean zooplankton persistence at a given level of zooplankton production. I used a larval gizzard shad food consumption model to predict consumption by different densities of 25-mm
gizzard shad (Dettmers and Stein 1992), from which I established the range of fish densities to be added to enclosures. Specific fish densities were calculated such that their estimated zooplankton consumption bounded preliminary estimates of crustacean zooplankton production in a random sample of enclosures (N = 3 per lake) just before fish were added. Gizzard shad (23 mm TL) were collected with buckets and immediately added to enclosures on June 13, 1991 (Kokosing), June 16, 1992 (Clark), and June 18, 1992 (Knox). This design provided a realistic test of the capacity for crustacean zooplankton communities protected from predation for 5 weeks to persist in the face of gizzard shad consumption. Based on previous experience handling 25-mm gizzard shad, I assumed handling mortality to be 25-30%; thus, I added 0, 7, 13, and 26 fish·m"-3 to Kokosing enclosures, 0, 16, 32, and 62 fish·m"-3 to Clark enclosures, and 0, 4, 8, and 16 fish·m"-3 to Knox enclosures to generate my expected treatment densities. I evaluated estimated handling mortality at the time of gizzard shad addition in each lake by adding 50 fish into each of two 120-L containers. After 24 h, I drained the containers and counted and measured surviving fish to estimate mortality and the initial size of the gizzard shad. Final treatment densities differed from expected densities due to differences in gizzard shad survival among enclosures.
All enclosures were inspected weekly for holes. High winds caused holes to develop rapidly at or within 10 cm of the water line in most enclosures in Clark and Knox lakes (1992). Beginning on May 28, I used waterproof tape to repair holes and reinforce weak areas. By the time gizzard shad were added, no new holes had developed. However, during May 28-June 16, larval gizzard shad entered all enclosures in Clark Lake and nine enclosures in Knox Lake by moving from the lake through holes in enclosures. With a spotlight at night, I found 1-6 gizzard shad in Clark Lake enclosures, and 1-3 shad in Knox Lake enclosures designated to receive gizzard shad.

Because gizzard shad could not be removed without destroying the enclosures, I did not adjust the gizzard shad addition scheme, except to be certain that I had fishless bags in Knox Lake. In Knox Lake, I allowed the nine enclosures already containing gizzard shad to receive additional gizzard shad according to my original design (Table 5).

Gizzard shad consumed crustacean zooplankton for 4-5 weeks in the enclosures. In Kokosing Lake, I counted zooplankton from June 12 to July 10. After July 10, 6 of 12 enclosures were destroyed in a wind storm. I collected data for overall fish survival and growth when the remaining intact enclosures were drained on July 24-25, 1991. Enclosures were drained on July 15, 1992 in Knox Lake and on
July 21, 1992 in Clark Lake. All remaining gizzard shad were counted and measured (nearest mm).

To compare dynamics of organisms in the lake with those in enclosures, I collected crustacean zooplankton and ichthyoplankton weekly from Kokosing Lake May 3-October 1, 1991, from Clark Lake May 7-September 26, 1992, and from Knox Lake May 4-August 11, 1992. Zooplankton were collected from three sites per lake with a 2-m tube sampler (33.5 L per site) filtered through a 54-μm mesh net; densities were averaged across sites to generate a mean for each date. I collected ichthyoplankton by towing a 0.75-m diameter, metered ichthyoplankton net (500-μm mesh) at the surface at 1.0-1.5 m·s⁻¹ for 3-5 min; two replicate tows were taken on each date. Larvae were preserved immediately in 10% formalin, returned to the laboratory, and identified, counted, and measured (up to 50 per species, nearest mm TL).

Only crustacean zooplankton were counted in the laboratory (Stahl and Stein 1994); hence, in the remaining text, zooplankton equates to crustacean zooplankton. Up to 20 individuals of each taxon in a sample were measured (nearest 0.01 mm) with a digitizing tablet viewed through a microscope drawing tube. These measurements provided size distributions through time and allowed me to calculate biomass from taxon-specific, length-dry weight regressions (Dumont et al. 1975; Bottrell et al. 1976; G. G. Mittelbach, Kellogg Biological Station, Michigan State University,
unpublished data). Phytoplankton were concentrated by filtering through a 0.45-μm filter, placed on a cover slip, and cleared with 2-hydroxypropyl methacrylate. Cover slips were then dried for 12 h, mounted to a slide (N=3 slides per sample), and counted using an Olympus BH-2 compound microscope with Nomarski optics at 200x and 400x. At least 15 fields were counted at each magnification to achieve a coefficient of variation of < 10% (St. Amand 1990).

I calculated zooplankton production as the increase in mass of existing individuals plus the number of eggs produced each week (Culver and DeMott 1978). Temperature-dependent growth and egg development equations were used to determine the time individuals spent in each stage (DeMott 1976; Bean 1980). Zooplankton growth plus fecundity provided production estimates for each taxon. Taxon-specific production was then summed across taxa to generate estimates of total zooplankton production for each weekly interval.

I analyzed treatment effects for total zooplankton density, size, biomass, production, and taxon-specific density via split-plot repeated-measures analysis of variance (Maceina et al. 1994). Treatment effects were compared from the last date that all enclosures were fishless (mid-June), until I ended experiments (mid-July). Data for zooplankton density, biomass, production, edible phytoplankton biomass, and inedible phytoplankton biomass
were log(x + 1)-transformed before statistical analysis to reduce heteroscedasticity and generate normally distributed residuals.

Results

Enclosure Experiments

I used the mean edible phytoplankton biovolume in enclosures during June-July to characterize productivity among lakes. Edible phytoplankton biovolume differed among enclosures from the three lakes (ANOVA, F=14.22; df=1,165; P<0.0001; see Figures 10, 13, and 14). Clark Lake enclosures were most productive, providing twice the biovolume of edible phytoplankton than Kokosing Lake enclosures, and four times that of Knox Lake enclosures.

Based on open-lake samples from Clark Lake, zooplankton did not peak during spring, never exceeding 100 individuals·L⁻¹ through June 28 (Figure 10a). Zooplankton density peaked at 187·L⁻¹ on July 11, compared to zooplankton peaks of > 400·L⁻¹ in all enclosures. Dominant zooplankton in the lake were cyclopoid copepods, calanoid copepods, and copepod nauplii. Larval gizzard shad first appeared on May 13, reaching a peak density of 38·m⁻³ on June 28, with a secondary peak of 24·m⁻³ on May 27 (Figure 10a).

Zooplankton density in Clark Lake enclosure treatments initially was < 75·L⁻¹ during May 12-19, increasing to > 300·L⁻¹ during May 20–June 9, and remaining above that level
through June 16, after which gizzard shad were added to enclosures (Figure 10b). *Daphnia* spp., copepod nauplii, and calanoid copepods were dominant; cyclopoid copepods and *Bosmina* spp. generally were rare. Thus, enclosure zooplankton communities differed from the lake in that they supported more *Daphnia* spp. and fewer cyclopoid copepods.

In enclosures, mean treatment densities, based on recovery of gizzard shad from enclosures, were 12 (N=4), 31 (N=4), 43 (N=4), and 41 (N=4) fish·m⁻³. Survival (mean ± 1 SE) during June 16-July 21, 1992, pooled across treatments and corrected for fish known to be in enclosures before the manipulation, was 88.7 ± 6.6%.

After gizzard shad addition, zooplankton abundance differed among treatments (Figure 10b; Table 6); zooplankton were less abundant in all enclosures to which I added gizzard shad, than in enclosures without added gizzard shad (Tukey's multiple comparisons, \( P<0.05 \)). Zooplankton declined through time in all treatments, but declined more rapidly when gizzard shad were added (Figure 10b; Table 6). Both calanoid copepods and *Daphnia* spp. declined substantially.

Dynamics of zooplankton biomass (Table 6) and production (Table 6; Figure 11a) mimicked zooplankton density patterns in response to gizzard shad. Crustacean zooplankton size declined through time, but did not differ across gizzard shad densities (Figure 10c; Table 6).
Edible phytoplankton biovolume (primarily *Scenedesmus* spp., *Cryptomonas* spp., *Euglena* spp., and *Cyclotella* spp.) differed among treatments and through time (Figure 10d; Table 7); edible phytoplankton biovolume was greatest in the treatment to which I added the most gizzard shad (Tukey’s multiple comparisons, *P*<0.05). Inedible phytoplankton (primarily *Oscillatoria* spp., *Synedra* spp., *Cosmarium* spp., and *Closterium* spp.) did not differ among treatments, although biovolume varied slightly through time (Table 7).

Because gizzard shad invaded all enclosures and I could not maintain consistent gizzard shad densities within treatments, I also analyzed these results by regression. Zooplankton density was inversely related to gizzard shad density beginning the second week following gizzard shad addition. By July 21, the regression explained 83% of the existing variance in zooplankton density across enclosures (*ln*(zooplankton+1) = 7.49-1.69*ln*(gizzard shad+1); Figure 12a).

Zooplankton did not peak in Kokosing Lake during spring and never exceeded 45 individuals·L⁻¹ (Figure 13a), whereas zooplankton peaks of >500·L⁻¹ occurred in 11 of 12 enclosures. Dominant zooplankton in the lake were *Diaphanosoma* spp., cyclopoid copepods, calanoid copepods, and copepod nauplii. Larval gizzard shad first appeared on May 16, reaching a peak density of 15·m⁻³ on May 23, with a secondary peak on June 5 (Figure 13a). By June 12, most
larval gizzard shad had metamorphosed into juveniles (> 25 mm TL) that could avoid the collection gear.

Zooplankton density in Kokosing Lake enclosure treatments initially was < 5·L⁻¹ during May 8-22, increasing to > 500·L⁻¹ during June 5-June 12, just before gizzard shad addition (Figure 13b). *Bosmina* spp., copepod nauplii, and cyclopoid copepods were dominant; calanoid copepods and *Daphnia* spp. generally were rare. *Bosmina* spp. were a greater proportion of the zooplankton community in enclosures, whereas calanoid copepods were more abundant in the lake.

Final gizzard shad treatment densities, based on recovery from intact enclosures, were 0 (N=2), 4 (N=1), 9 (N=2), and 17 (N=1) fish·m⁻³. Survival during June 13-July 26, 1991, pooled across treatments, was 63.9 ± 3.6%.

After juvenile gizzard shad addition, zooplankton differed marginally among treatments (Figure 13b; Table 6). Fewer zooplankton occurred with 20 gizzard shad·m⁻³ than in fishless enclosures (Tukey’s multiple comparisons, *P* < 0.05). Although zooplankton abundance declined through time in all treatments, it declined more rapidly when combined with gizzard shad (Figure 13b; Table 6). Calanoid and cyclopoid copepods, as well as *Daphnia* spp., were the taxa most strongly reduced by gizzard shad. Regression analysis of zooplankton remaining versus gizzard shad recovered from enclosures revealed that these variables were negatively
related beginning 2 weeks after gizzard shad addition. On July 10, gizzard shad abundance explained 97% of the variability in zooplankton density across enclosures \((\ln(\text{zooplankton}+1) = 6.12-1.28*\ln(\text{gizzard shad}+1));\) Figure 12b).

Zooplankton biomass differed among treatments (Table 6), being greatest in fishless enclosures (Tukey's multiple comparisons, \(P<0.05\)). Although biomass declined through time, the rate of decline differed only slightly among treatments (Table 6). Zooplankton production declined in all treatments containing gizzard shad (Table 6; Figure 11b; Tukey's multiple comparisons, \(P<0.05\)), and through time (Table 6). Zooplankton size did not differ among treatments, but varied through time (Figure 13c; Table 6).

Phytoplankton responses were not as dramatic as in Clark Lake. Neither edible (primarily *Scenedesmus* spp. and *Euglena* spp.) nor inedible (primarily *Cosmarium* spp., *Mougeotia* spp., and *Synedra* spp.) phytoplankton biovolume differed among treatments (Figure 13d; Table 7). However, both fractions varied through time (Table 7).

Zooplankton were abundant in Knox Lake, peaking at > 1,100 organisms·L\(^{-1}\) on May 27. Zooplankton remained > 300·L\(^{-1}\) through June 25, after which they crashed (Figure 14a). Larval gizzard shad first appeared on May 20; their abundance peaked on June 3 (Figure 14a), and larvae were
present through June 24. Peak larval gizzard shad abundance closely mimicked the timing of the zooplankton peak.

Zooplankton density in Knox Lake enclosures before gizzard shad were added mimicked lakewide trends. Initially, abundance was < 76·L⁻¹ during May 13-20, increasing to > 260·L⁻¹ during May 21-28 (Figure 14b). Zooplankton abundance remained > 300·L⁻¹ during May 29-June 18, when gizzard shad were added to enclosures. Bosmina spp. were dominant; calanoid copepods, copepod nauplii, Daphnia spp., and Chydorus spp. were common but less abundant.

Final treatment densities, based on recovery of gizzard shad from enclosures, were 0 (N=3), 5 (N=4), 7 (N=4), and 11 (N=4) fish·m⁻³. Survival during June 18-July 15, 1992, pooled across treatments and corrected for fish known to be in enclosures before the manipulation, was 74.3 ± 8.0%.

Zooplankton abundance differed among treatments (Figure 14b; Table 6), with fewer zooplankton in enclosures containing gizzard shad (Tukey's multiple comparisons P<0.05). Although zooplankton declined through time in all treatments, it declined more rapidly with gizzard shad (Figure 14b; Table 6). Bosmina spp. and calanoid copepod populations were most strongly affected by gizzard shad. Regression analysis revealed that gizzard shad abundance explained 74% of the existing variance in zooplankton
remaining in enclosures on July 15 ($\ln(\text{zooplankton}+1) = 3.49-1.94\ln(\text{gizzard shad} + 1)$; Figure 12c).

Dynamics of zooplankton biomass (Table 6) and production (Figure 11c; Table 6) followed zooplankton density patterns. Mean zooplankton size varied with time, and differed slightly among treatments, with zooplankton size in fishless enclosures tending to be larger (Figure 14c; Table 6).

Neither edible (Cymbella spp. and Scenedesmus spp.) nor inedible (Spirogyra spp. and Mougeotia spp.) phytoplankton biovolume differed among treatments (Figure 14d; Table 7). The edible fraction varied through time; the inedible fraction did not (Figure 14d; Table 7).

Understanding Zooplankton Productivity and Persistence

Final zooplankton density in enclosures was negatively related to gizzard shad density and positively related to zooplankton production. I generated a response surface using data from 36 enclosures across the three lakes to interpolate across the range of my data with the SigmaPlot graphics package (Figure 15). Regression analysis using lake as an indicator variable explained > 94% of the observed variation in zooplankton remaining in enclosures by accounting for gizzard shad density, zooplankton production, and lake-to-lake differences (Table 8). This analysis revealed that final zooplankton abundance was influenced negatively by gizzard shad density and positively by crustacean zooplankton production (Figure 15). Although
zooplankton abundance and zooplankton production may be correlated, this analysis describes those conditions necessary for zooplankton persistence. Adding phytoplankton concentration and interaction terms to this model provided no additional explanatory power to the observed pattern of zooplankton abundance.

I then assessed these lake-to-lake differences, and discovered that Clark and Kokosing lakes were similar, but differed from Knox Lake (Table 8). In Knox Lake, gizzard shad abundance was less strongly correlated with final zooplankton abundance than zooplankton production. In Clark Lake, gizzard shad and zooplankton production affected final zooplankton abundance similarly. In Kokosing Lake, gizzard shad density controlled zooplankton dynamics.

Peak zooplankton densities exceeding 800·L⁻¹ occurred in several enclosures in each lake before gizzard shad were added, despite differences in productivity among lakes. These peak zooplankton densities responded quite differently to the range of gizzard shad consumption present in enclosures. To explain why zooplankton remained more abundant in Clark Lake enclosures than in enclosures from other lakes, I examined final zooplankton density in enclosures. If final zooplankton density differed when final gizzard shad density was similar across enclosures, I might expect nutrient-related factors to be responsible for the observed differences. I only compared enclosures
containing 3-12 gizzard shad·m⁻³, densities common to all experiments. In this subset of enclosures, mean gizzard shad density was similar across enclosures (Clark=6.5, Kokosing=7.3, Knox=5.9). Zooplankton density differed across enclosures (ANOVA, F=261.66; df,2,12; P<0.0001), with most zooplankton remaining in Clark Lake (mean=98.6·L⁻¹), some in Kokosing Lake (mean=28.0·L⁻¹), and few in Knox Lake (mean=1.0·L⁻¹). These results suggest nutrient or bottom-up influences were important.

To assess how bottom-up processes influenced zooplankton in the face of planktivore consumption, I examined the seasonal ratio of zooplankton births to deaths (ratio=0.88 in Clark Lake; 0.35 in Knox Lake; 0.28 in Kokosing Lake). This ratio differed among lakes (ANOVA, F = 8.29, df, 2,167, P = 0.0004) and was greatest for Clark Lake enclosures (Tukey’s multiple comparisons, P < 0.05), suggesting that conditions for zooplankton were more favorable in Clark Lake enclosures.

I also examined the seasonal ratio of edible:inedible phytoplankton biovolume (E:I) in enclosures across lakes to assess food quality for zooplankton. This ratio differed among lake and enclosure combinations (ANOVA, F=80.00; df,2,165; P<0.0001), and was greatest in Clark Lake enclosures (E:I=3.9), intermediate in Kokosing enclosures (E:I=1.6), and lowest in Knox enclosures (E:I=0.3), suggesting that food quality, in addition to gizzard shad
predation, likely determined mortality of zooplankton across lakes.

Discussion

Age-0 gizzard shad (23-90 mm TL) eliminated crustacean zooplankton from enclosures within 2-3 weeks in all experiments. Although I varied gizzard shad density > 15-fold across all treatments, I found few differences among treatments containing gizzard shad. Regardless of productivity, zooplankton were nearly eliminated when > 12 gizzard shad·m⁻³ occurred. Zooplankton persisted > 100·L⁻¹, that density required for larval fish survival (Werner and Blaxter 1980; Eldridge et al. 1981; Li and Mathias 1982), only when zooplankton production exceeded 220 mg·m⁻³·d⁻¹ and gizzard shad abundance was < 10·m⁻³. Size-selective predation by gizzard shad on zooplankton did not occur. Top-down effects cascaded to phytoplankton only in those enclosures with Daphnia spp. densities initially > 40·L⁻¹ and abundant edible algae.

Enclosure results mimicked the lakewide zooplankton trends only in Knox Lake, suggesting that zooplankton in Knox Lake persisted in the face of larval gizzard shad consumption. However, as gizzard shad grew > 25 mm, the consumptive demand of gizzard shad probably overwhelmed the production of zooplankton, causing their collapse (Dettmers and Stein 1992). The rate and timing of this decline was
quite similar to the timing of the zooplankton collapse in enclosures after the addition of 23-mm gizzard shad.

In Clark and Kokosing lakes, zooplankton density remained low relative to densities observed in enclosures before gizzard shad were added. Perhaps this difference resulted from additional predation pressure on zooplankton resulting from 1) abundant adult gizzard shad and 2) other planktivores that increased consumptive demand on zooplankton in spring. Unfortunately, I have no direct evidence that populations of adult gizzard shad or other planktivores were abundant in Clark and Kokosing lakes but rare in Knox Lake. However, in Lake Mendota, abundant cisco *Coregonus artedi* populations could account for the observed *Daphnia* spp. mortality during April-September 1987, except for 2-3 weeks in late May-early June (Luecke et al. 1992). Thus, it is possible that adult fishes maintained zooplankton at low levels via predation in these reservoirs. Given that my enclosures protected crustacean zooplankton from all predation sources, I believe this test with enclosures strengthens my conclusion that age-0 gizzard shad can eliminate reservoir zooplankton. This extreme reduction of zooplankton contrasts with results from north temperate lakes. For example, zooplankton dramatically increased in Lake St. George, Ontario, Canada, following a winterkill that eliminated piscivores (McQueen et al. 1989). A large
year-class of planktivores subsequently reduced zooplankton biomass.

Zooplankton were still more abundant in Lake St. George (biomass reduced to about 1,500 mg·m⁻³) than in this study (biomass reduced to < 50 mg·m⁻³). Perhaps the biomass of planktivores used in this study equaled or exceeded those of McQueen et al. (1989), thus probably exerting a greater consumptive demand on zooplankton and forcing them to even lower levels. Gizzard shad probably maintain their high biomass in reservoirs because they can feed successfully on detritus, which allows them to persist in the face of low zooplankton resources.

However, planktivore biomass (cisco and yellow perch estimated biomass=200 kg·ha⁻¹) in Lake Mendota before the 1987 cisco die-off equaled or exceeded final gizzard shad biomass in 25 of 44 enclosures (Rudstam et al. 1992). Yet, in Lake Mendota, zooplankton was more abundant than in this study. Thus, planktivore biomass does not completely explain the differences in zooplankton abundance observed between natural lakes and these reservoirs.

Enclosure effects also could have artificially increased the impact of gizzard shad on zooplankton because detritus was unavailable to gizzard shad. I think this is unlikely because (1) zooplankton abundance in these reservoirs either remained low or declined at rates similar to my enclosures and (2) extensive periphyton growth occurred in the
enclosures, providing gizzard shad with an alternative food resource.

Gizzard shad detritivory also may explain poor zooplankton persistence in my enclosures. Given their capacity to switch from zooplankton to feed on phytoplankton and detritus (Miller 1960; Bodola 1966), gizzard shad are more weakly linked to zooplankton than northern planktivores (even those that rely partially on benthos) because detritus in most Ohio reservoirs is essentially unlimited. Thus, gizzard shad eliminate crustacean zooplankton, and then simply switch to detritus to maintain high population biomass.

Zooplankton and phytoplankton did not seem linked in my age-0 gizzard shad experiments. Only when *Daphnia* spp. were abundant in enclosures (averaging > 40 L⁻¹ during June-July experiments) did I document reduced edible phytoplankton biovolume in enclosures to which I added gizzard shad. This is consistent with observations in northern lakes, where piscivore responses cascade to phytoplankton, but only when *Daphnia* spp. are abundant (Carpenter et al. 1987; Leibold 1989). Large-bodied grazers seem essential to improve water clarity by top-down manipulations.

**Management Implications**

I see little potential for reduced gizzard shad abundance to improve reservoir water clarity by top-down forces. Because most reservoir turbidity is inorganic in
nature, it probably will be substantially modified only by altered land use practices and improved riparian buffers. Reservoirs also tend to be dominated by small crustacean zooplankton that, even if abundant, probably have little impact on phytoplankton. Finally, gizzard shad may reduce water clarity by consuming sediments and resuspending nutrients that otherwise would be unavailable to phytoplankton, thus increasing phytoplankton biomass (Vanni 1995). It is unrealistic to expect improved water clarity in reservoirs with abundant gizzard shad, small crustacean zooplankton, and agricultural watersheds.

However, some potential exists to reduce gizzard shad populations to the point that zooplankton abundance remains sufficiently high to improve recruitment of planktivorous sport fishes (Dettmers et al., in press). Sport fishes with early planktivorous life stages frequently suffer poor recruitment when zooplankton abundance falls below $100 \cdot \text{L}^{-1}$ (Werner and Blaxter 1980; Eldridge et al. 1981; Li and Mathias 1982). Because gizzard shad in reservoirs appear in the pelagic 2-3 weeks before bluegills *Lepomis macrochirus* and crappies (DeVries and Stein 1992; Welker et al. 1994), they can eliminate zooplankton and reduce recruitment of these sport fishes (DeVries and Stein 1992). Thus, if reservoir managers seek to improve sport fish recruitment, they must reduce gizzard shad to densities that maintain
zooplankton at densities > 100·L⁻¹ during open-water residence of larval fishes.

My response surface predicts only a small region where zooplankton abundance persists at > 100·L⁻¹ (ln(100)=4.6; Figure 15). Only when zooplankton productivity exceeds 220 mg·m⁻³·d⁻¹ (ln(220)=5.4) and age-0 gizzard shad density is < 10·m⁻³ (ln(10)=2.3) can zooplankton and gizzard shad coexist. In most Ohio reservoirs, even < 10 gizzard shad·m⁻³ can eliminate crustacean zooplankton. Historical sampling of 18 reservoirs by the Aquatic Ecology Laboratory (M. T. Bremigan, N. S. Donovan, and JMD, unpublished data) and the Ohio Division of Wildlife (M. Austin, Xenia, Ohio, personal communication) revealed peak densities of larval gizzard shad below 10·m⁻³ in 19 of 44 reservoir-years.

Increasing piscivore abundance could reduce gizzard shad abundance, permitting zooplankton to increase in more productive reservoirs. Nevertheless, in Ohio reservoirs, largemouth bass annually consume 30% or less of the gizzard shad standing crop (Carline et al. 1984). I predict that age-0 gizzard shad abundance must be driven below 10·m⁻³ for crustacean zooplankton to persist at > 100·L⁻¹. Given the above rate of piscivore consumption, age-0 gizzard shad abundance could not exceed 14·m⁻³ in even the most productive reservoirs for piscivores to sufficiently reduce gizzard shad and improve sport fish recruitment.
Historical reservoir sampling revealed that in 25 of 44 lake-years, peak age-0 gizzard shad abundance was < 14 \cdot m^{-3} (Bremigan et al. 1991; N. S. Donovan, M. T. Bremigan, aquatic Ecology Laboratory, unpublished data). Thus, many reservoirs have the potential for increased zooplankton abundance resulting from low age-0 gizzard shad density. However, when one considers zooplankton productivity, this conclusion changes. Historical sampling indicates that zooplankton production in reservoirs exceeded 220 mg \cdot m^{-3} \cdot d^{-1} only in 3 of 10 lake-years (M. T. Bremigan and JMD, Aquatic Ecology Laboratory, unpublished data). Given that only Clark Lake enclosures maintained sufficient zooplankton production to sustain abundant zooplankton, I believe that only about 1 of 8 reservoirs might sustain sufficient zooplankton production to permit zooplankton persistence at > 100 \cdot L^{-1}. Thus, stocking piscivores in Ohio to reduce gizzard shad abundance unlikely will increase zooplankton density to support increased recruitment of sport fishes, except in reservoirs with age-0 gizzard shad abundance < 10 \cdot m^{-3} and zooplankton production > 220 mg \cdot m^{-3} \cdot d^{-1}.
Literature Cited


Welker, M. T., C. L. Pierce, and D. H. Wahl. 1994. Growth and survival of larval fishes: roles of competition and

Table 5. Design of enclosure experiments in three Ohio reservoirs, 1991-1992. Reservoirs were chosen to reflect the range of zooplankton productivity in Ohio. A larval gizzard shad food consumption model (Dettmers and Stein 1992; see text for details) was used to determine age-0 gizzard shad (23 mm total length) densities that provided an increasing challenge to zooplankton production in each reservoir.

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Table 7. Summary of split-plot repeated measures ANOVA results for log-transformed responses of phytoplankton biovolume to increased age-0 gizzard shad abundance in enclosures in Clark, Kokosing, and Knox lakes, Ohio, June-July 1991 and 1992.

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\textsuperscript{a} Sub-plot error term

\textsuperscript{b} Main-plot error term
Table 8. Regressions predicting zooplankton density remaining in enclosures, for given gizzard shad density and zooplankton production levels, across all enclosures from all reservoirs, and for each reservoir. The regression model incorporating data from all reservoirs was \( \ln(\text{zooplankton density}) = a + b\ln(\text{gizzard shad density}) + c\ln(\text{zooplankton production}) + d\text{reservoir} \). Partial regressions for gizzard shad density and zooplankton production are presented for each reservoir. Regressions for Clark and Kokosing lakes were similar \( (P=0.19) \), but both differed from the relationship in Knox Lake enclosures \( (P<0.0001) \).

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| Knox     | -1.06| -0.28| 0.84| 123.91 | <0.0001 | 0.95|
| N=15     | 3.49 | -1.94| 24.40| <0.0001| 0.63    |
|          | -1.70| 0.93| 239.93| <0.0001| 0.95    |

| All      | 3.79 | -0.63| 0.72| 185.20 | <0.0001 | 0.94|
| reservoirs* |   |     |    |        |         |     |
| N=36     |   |     |    |        |         |     |

* The equation for all reservoirs also includes the coefficient d (see table legend), calculated to be -1.31.
Figure 10. Mean (± 1 SE) crustacean zooplankton and larval gizzard shad abundance (A) in Clark Lake, Ohio, April 23-September 2, 1992; mean crustacean zooplankton abundance in enclosure treatments (B), May 14-July 21, 1992; mean crustacean zooplankton size (C); and mean edible phytoplankton biovolume (D), June 16-July 21, 1992. Arrows indicate the date gizzard shad were added to enclosures. For experimental design details, see Table 5.
Figure 10
Figure 11. Mean (± 1 SE) crustacean zooplankton production in enclosure treatments at Clark Lake, Ohio, June 16-July 21, 1992 (A); Kokosing Lake, Ohio, June 12-July 10, 1991 (B); and Knox Lake, Ohio, June 18-July 15, 1992 (C). Arrows indicate the date gizzard shad were added to enclosures. For experimental design details, see Table 5.
Figure 11

A. Clark Lake
- 12 Shad·m⁻³
- 31 Shad·m⁻³
- 43 Shad·m⁻³
- 41 Shad·m⁻³

June 16 June 23 June 30 July 6 July 14 July 21

B. Kokosing Lake
- 0 Shad·m⁻³
- 4 Shad·m⁻³
- 9 Shad·m⁻³
- 17 Shad·m⁻³

June 12 June 19 June 26 July 3 July 10

C. Knox Lake
- 0 Shad·m⁻³
- 5 Shad·m⁻³
- 7 Shad·m⁻³
- 11 Shad·m⁻³

June 18 June 24 July 1 July 7 July 15
Figure 12. Plots of the relationship between zooplankton density and gizzard shad density in enclosures on the last day of experiments, i.e., (A) after 35 d in Clark Lake, on July 21, 1992; (B) after 27 d in Kokosing Lake, on July 10, 1991; and (C) after 27 d in Knox Lake, on July 15, 1992. See Table 8 for the specific regression relationships.
Figure 12

A. Clark Lake: Day 35
   \( N = 15 \)

B. Kokosing Lake: Day 27
   \( N = 6 \)

C. Knox Lake: Day 27
   \( N = 15 \)

Zooplankton Density (Number L\(^{-1}\))

Gizzard Shad Density (Number m\(^{-3}\))
Figure 13. Mean (± 1 SE) crustacean zooplankton and larval gizzard shad abundance (A) in Kokosing Lake, Ohio, May 10-August 2, 1991, mean crustacean zooplankton abundance in enclosure treatments (B), May 23-July 10, 1991; mean crustacean zooplankton size (C); and mean edible phytoplankton biovolume (D), June 12-July 10, 1991. Arrows indicate the date gizzard shad were added to enclosures. Note the x-axis scale differs among panels. For experimental design details, see Table 5.
Figure 13

A. Zooplankton and Larval Gizzard Shad Density

B. Enclosures

C. Enclosures

D. Edible Phytoplankton Biolume

Figure 13
Figure 14. Mean (± 1 SE) crustacean zooplankton and larval gizzard shad abundance (A) in Knox Lake, Ohio, April 23-August 27, 1992, mean crustacean zooplankton abundance in enclosure treatments (B), May 14-July 15, 1992, mean crustacean zooplankton size (C), and mean edible phytoplankton biovolume (D), June 18-July 15, 1992. Arrows indicate the date gizzard shad were added to enclosures. Note the x-axis scale differs among panels. For experimental design details, see Table 5.
Figure 14
Figure 15. Response surface of zooplankton remaining in enclosures at the end of each experiment versus the number of gizzard shad retrieved from each enclosure and final zooplankton production for Kokosing, Clark, and Knox lakes, Ohio. Arrows and associated numbers highlight the critical values of zooplankton production and gizzard shad density necessary for zooplankton to persist at $> 100 \cdot L^{-1}$. 
Figure 15
CHAPTER V
EXPLORING POTENTIAL REGULATION OF AGE-0 GIZZARD SHAD
BY HYBRID STRIPED BASS IN RESERVOIRS

Introduction

The trophic cascade hypothesis provides an excellent framework for assessing food web interactions in aquatic systems (Carpenter et al. 1985; McQueen et al. 1989; Carpenter and Kitchell 1993). In particular, abundant piscivores consume planktivores, permitting increased zooplankton size and abundance, and reducing phytoplankton abundance (Carpenter et al. 1987). This suite of trophic interactions is quite predictable and frequently occurs in north temperate lakes (Carpenter et al. 1987; McQueen et al. 1989; but see DeMelo et al. 1992). Managers can take advantage of these top-down effects not only to increase piscivore abundance (potentially improving the fishery; Kitchell 1992), but also to increase crustacean zooplankton (potentially improving recruitment of sport fishes; Stein et al., in press; Dettmers et al., in press) and reduce phytoplankton (increasing water clarity; Carpenter et al. 1987).

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In reservoirs, gizzard shad *Dorosoma cepedianum* frequently dominates fish community biomass (Timmons et al. 1978; Miranda 1983; Willis and Jones 1986) because this species exhibits high fecundity (Vondracek and LeHew 1991), rapid growth, and limited vulnerability to piscivores (Adams and DeAngelis 1987; Johnson et al. 1988; Hambright et al. 1991; Stein et al., in press). Simultaneously, gizzard shad imposes its own control on lower trophic levels (Drenner et al. 1982a,b; Dettmers and Stein 1992; DeVries and Stein 1992), without in turn being resource-limited by zooplankton or phytoplankton. Age-0 gizzard shad > 25 mm TL can eliminate crustacean zooplankton populations (Dettmers and Stein 1992; DeVries and Stein 1992) before switching to phytoplankton and detritus (Miller 1960; Bodola 1966). Further, as age-0 gizzard shad grow from 30 to 60 mm, the proportion of zooplankton they consume declines, remaining low for individuals > 60 mm (Yako et al. in review). Thus, gizzard shad < 60 mm are most likely to regulate crustacean zooplankton abundance. In so doing, these gizzard shad compromise the recruitment environment of sport fish whose larvae depend on limited zooplankton during May-July. If piscivores are to exert top-down effects that generate increased crustacean zooplankton in reservoirs, then this size class of gizzard shad must be regulated.

In Ohio reservoirs, consumption of gizzard shad by resident piscivores accounted for only 20-30% of annual
gizzard shad production (Carline et al. 1984; Johnson et al. 1988), providing little opportunity for increasing zooplankton by reducing gizzard shad. However, introduced piscivores, e.g., hybrid striped bass *Morone saxatilis* x *M. chrysops*, potentially can control shad populations in reservoirs, increasing zooplankton abundance and perhaps improving recruitment of planktivorous sport fishes. In 0.4-ha ponds simulating reservoirs, hybrid striped bass reduced age-0 gizzard shad abundance in a five-week experiment, permitting crustacean zooplankton to persist at > 100·L⁻¹, a minimum density required for successful recruitment, if age-0 gizzard shad abundance is < 10·m⁻³ and zooplankton production exceeds 220 mg·m⁻³·d⁻¹ (Dettmers et al., in press). As large, open-water piscivores, hybrid striped bass may provide the best opportunity for control of nuisance gizzard shad populations.

The potential for control of prey populations depends in part on the sizes of prey eaten by piscivores. For instance, if piscivores prefer to consume gizzard shad < 60 mm, they are more likely to permit increased zooplankton abundance. From 32 laboratory and field studies that quantified piscivore prey preference, piscivores almost universally (91 of 93 cases) selected prey sizes equal to or smaller than the average size available (Juanes 1994). More specifically, hybrid striped bass selected smaller gizzard shad than were available in ponds (Dettmers et al., in
press) and rarely ate gizzard shad > 65 mm in West Point Reservoir (Ott and Malvestuto 1981), patterns that may derive from differential size-based capture success favoring small prey.

Incorporating these piscivore diet patterns into bioenergetics models, prey population responses can be predicted, given piscivore growth rates. For example, bioenergetics modeling applied to Lake Michigan predicted that salmonine consumption owing to high stocking rates in the early 1980's could conceivably collapse the alewife Alosa pseudoharengus prey base (Stewart et al. 1981).

To assess the potential for piscivore-mediated increases in zooplankton abundance, I require information on piscivore size selectivity and consumptive demand. Here, I quantify size selection patterns of hybrid striped bass feeding on age-0 gizzard shad and then use a bioenergetics model to explore consumptive demand of hybrid striped bass to assess the potential for these piscivores to increase zooplankton abundance by reducing age-0 gizzard shad.

Methods

Laboratory Experiments

I conducted 30-min experiments in a 2.0 x 0.5 x 0.5 m, 500-L tank at 17-21°C with 12 h light:12 h dark. The tank was divided into a predator chamber (440 L) and a prey chamber (60 L) by an opaque divider. With a window (1.35x0.30 m) in the tank, covered by one-way glass and a
mirror (1.42x0.41 m) at a 45° angle above the tank a predator could be observed throughout the tank from the side or from above.

Hybrid striped bass were collected from the Hebron State Fish Hatchery and Buckeye Lake, Licking, Fairfield, and Perry counties, Ohio. To assess the maximum size range of prey that could be consumed, I measured their total length, mouth depth, and mouth width. Once in the laboratory, hybrid striped bass were fed gizzard shad and fathead minnows *Pimephales promelas*. For gizzard shad collected from nearby reservoirs, total length and body depth were measured so as to determine how total length and body depth were related. In the laboratory, gizzard shad were fed *Artemia* nauplii and commercial fish food, whereas fathead minnows were fed only commercial fish food.

To quantify size selection by hybrid striped bass, I combined a single individual with 15 gizzard shad (5 individuals x 3 size classes) in each trial. Gizzard shad were combined with piscivores in three separate combinations of three size classes each (Table 9). I included gizzard shad within a size class if they were ± 5 mm of the nominal size (e.g., 40 mm size class: 35-45 mm). I used two sizes of hybrid striped bass: large (310-360 mm) and small (190-250 mm). Individual piscivores were starved for 24 h before each trial.
Gizzard shad were added to the prey chamber 15 min before each experiment. Prey were combined with the piscivore by removing the divider, creating a single experimental chamber. I quantified attacks and captures by the piscivore; capture efficiency was calculated as the capture divided by number of attacks. Experiments ended after 30 min or upon consumption of one gizzard shad. Remaining gizzard shad were then removed and measured.

One to five individuals per piscivore size class were tested, with three to five trials per predator; I then compared means for each fish to avoid pseudoreplication. Whether hybrid striped bass preferred prey sizes was tested with a Chi-square contingency test. I used one-way ANOVA with Tukey’s multiple comparisons to evaluate capture efficiency, arc-sin transformed to approximate a normal distribution. Linear regression was used to describe relationships between total length and mouth gape or body depth.

Bioenergetics Model

I used a bioenergetics model (Hewett and Johnson 1992) to estimate hybrid striped bass growth and food consumption. The model runs on a daily time step and uses the following balanced energy relationship

\[ G = C - (R + S + F + U) \]

where growth \( G \) is expressed as energy consumed \( C \) minus the costs of metabolism \( R \), specific dynamic action \( S \),
egestion (F), and excretion (U). I used the model parameters developed for striped bass (Hartman and Brandt 1993), except that I increased $\theta_2$ and $\theta_3$ to 25°C and $\theta_4$ to 30°C to account for the increased optimal feeding temperature of hybrid striped bass (Woiwode and Adelman 1991).

I simulated the impact of a hybrid striped bass population consisting of three cohorts on age-0 gizzard shad in a generalized 65-ha Ohio reservoir with a mean depth of 2 m. Annual temperatures ranged from 4°C during December-March to 30°C for about 10 days in July; temperatures above 15°C occurred during June-October. Potential consumption of hybrid striped bass was estimated across three annual stocking rates: 125·ha$^{-1}$, the usual stocking rate of hybrid striped bass in Ohio waters (J. Marshall, Ohio Division of Wildlife, personal communication), which yielded a standing stock of 8 kg·ha$^{-1}$ after 3 years; 350·ha$^{-1}$ to achieve a standing stock after 3 years of 22 kg·ha$^{-1}$, the hybrid striped bass density used in 0.4-ha ponds to increase zooplankton density (Dettmers et al., in press); and 500·ha$^{-1}$ to achieve 32 kg·ha$^{-1}$ after 3 years, simulating a dense hybrid striped bass population. I assumed annual mortality was 90% during their first year of life (Stahl et al., in press) and 50% annually thereafter (King et al. 1979), with zero fishing mortality. Hybrid striped bass diets and growth were derived from Austin and Hurley (1987)
(see Table 10 for growth data). When hybrid striped bass consumed fish, I assumed that only gizzard shad were eaten, thus maximizing the impact of hybrid striped bass on gizzard shad. I further assumed that hybrid striped bass ate age-0 gizzard shad only after they grew larger than 20 mm; as such, I only explore hybrid striped bass predation post June 1.

To further bracket the potential piscivore impact, I evaluated hybrid striped bass consumption against two age-0 gizzard shad annual mortality schedules: 99 and 99.99%. This mortality range has been observed for juvenile fishes in marine and freshwater habitats (Dey 1981; Timmons et al. 1981; Crecco et al. 1983). Initial age-0 gizzard shad densities were 15, 25, and 38 m⁻³ to span a common range of age-0 gizzard shad densities in Ohio reservoirs that exceed 10 m⁻³ (Table 11).

**Results**

**Size Selection**

When exposed to the small combination of gizzard shad (Table 9; 17, 26, and 35% of predator body length, respectively; N=5 each), small hybrid striped bass preferred 40-mm prey (chi-square contingency test; df=2; \( P=0.0002 \); Figure 16). These smallest gizzard shad represented 78% of all prey eaten, whereas 80-mm gizzard shad never were consumed. Capture efficiency of small hybrid striped bass was marginally higher for 40-mm, as compared to 60-mm, prey
(ANOVA, F=5.24; df=1,6; P=0.06; Figure 17). Large hybrid striped bass (N=1) revealed no preference among sizes within the small gizzard shad combination (chi-square contingency test, df=2; P=0.78; Figure 16), despite consuming 40-mm prey in 50% of the trials. Attacks always ended with a capture for this predator size, regardless of prey size (Figure 17).

When feeding on the intermediate combination of gizzard shad (Table 9), small hybrid striped bass marginally preferred 60-mm prey (chi-square contingency test, df=2; P=0.06; Figure 16). These 60-mm prey comprised 60% of the prey eaten; 100-mm gizzard shad never were consumed. Unlike my results with the small gizzard shad combination, small hybrid striped bass captured 60- and 80-mm gizzard shad with similar efficiency when feeding on the intermediate combination of prey (ANOVA, F=0.04; df=1,4; P=0.84; Figure 17). Once again, large hybrid striped bass revealed no preference for particular sizes within the intermediate gizzard shad combination (chi-square contingency test, df=2; P=0.72; Figure 16); however, 44% of all prey consumed were 60 mm, whereas only 22% of prey consumed were as large as 100 mm. Capture efficiency did not differ across prey sizes for large hybrid striped bass (ANOVA, F=0.08; df=2,3; P=0.92; Figure 17).

Large hybrid striped bass (N=1) revealed no preference for a given prey size class when exposed to the large gizzard shad combination (chi-square contingency test, df=2;
though 60% of prey consumed were 80-mm fish. This predator was most efficient at capturing 100-mm prey and least efficient when capturing 120-mm prey (Figure 17).

Because hybrid striped bass exhibited little or no reduction in capture efficiency as prey size increased, I estimated the largest prey predators could consume. I derived a body depth vs. total length relationship for gizzard shad and a mouth width vs. total length relationship for hybrid striped bass to determine the size of prey relative to the limiting constraint of predator mouth gape.

Hybrid striped bass efficiently consumed prey that were at the morphological limits of consumption. For hybrid striped bass < 250 mm, this size was 80 mm (body depth=22 mm), whereas for hybrid striped bass 310-360 mm, this size was 120 mm (body depth = 32 mm). Both size classes of hybrid striped bass consumed gizzard shad of these respective sizes. Regressing capture efficiency against the proportion of the maximum gape for each prey, I found no relationship for either predator size (linear regression, F=0.07, df 1,8, P=0.80 for large hybrid striped bass and F=0.30, df 1,12, P=0.60 for small hybrid striped bass; Figure 18). Consequently, hybrid striped bass can consume prey whose limiting dimension equals their maximum gape without reduced capture efficiency, at least in a laboratory setting.
Bioenergetics Modeling

I evaluated the ability of hybrid striped bass to reduce age-0 gizzard shad < 60 mm to < 10·m⁻³ and thereby increase zooplankton density. My model estimated consumptive demand under three rates of hybrid striped bass stocking and two rates of age-0 gizzard shad mortality. Hybrid striped bass ate the most gizzard shad during June, when gizzard shad were smallest. Whereas predicted biomass of age-0 gizzard shad consumed increased through October, number of prey eaten by hybrid striped bass declined substantially as gizzard shad grew.

When peak age-0 gizzard shad abundance was 38·m⁻³, they did not decline to < 10·m⁻³ until October 1 if natural mortality was low (99%; Figure 19c) or until July 1 if mortality was high (99.99%; Figure 20c). Never did hybrid striped bass exert substantial predatory impact on these abundant prey when stocked at rates typically used by Ohio fishery managers.

Age-0 gizzard shad declined from a peak of 25·m⁻³ to < 10·m⁻³ on August 20 when natural mortality was low, and on June 15 when mortality was high (Figure 19b). At high mortality, hybrid striped bass eliminated age-0 gizzard shad by December 1 when stocked at rates ≥ 350·ha⁻¹ but did not appreciably change the date on which gizzard shad abundance fell below 10·m⁻³ (Figure 20b).
When peak age-0 gizzard shad density was 15 m⁻³, natural mortality reduced their abundance below 10 m⁻³ before hybrid striped bass began consuming gizzard shad, except at low natural mortality when gizzard shad fell below 10 m⁻³ on July 1 (Figure 19). Coupled with this low mortality rate, hybrid striped bass stocked at 500 ha⁻¹ reduced age-0 gizzard shad to < 10 m⁻³ on June 12 (Figure 19a). At high natural mortality, hybrid striped bass eliminated age-0 gizzard shad before December 1, regardless of stocking density (Figure 20a).

When natural gizzard shad mortality was low, hybrid striped bass never depleted age-0 gizzard shad by December 31 (Figure 19). Hybrid striped bass contributed only marginally to overall gizzard shad mortality when natural gizzard shad mortality was low because even the most densely stocked piscivores did not cause gizzard shad to fall below 10 m⁻³ before August 1 when gizzard shad initially were ≥ 25 m⁻³ (Figure 19). Under high natural gizzard shad mortality, hybrid striped bass stocked at ≥ 350 ha⁻¹ depleted gizzard shad, regardless of the initial gizzard shad abundance and hybrid striped bass stocked at 125 ha⁻¹ eliminated gizzard shad when they were initially abundant at ≥ 15 m⁻³ (Figure 20).

Discussion

I quantified size-selectivity by hybrid striped bass for gizzard shad, incorporated these data into a bioenergetics
model for the predator and determined that these piscivores are unlikely to regulate gizzard shad populations in small reservoirs as exemplified by our systems in Ohio. Small hybrid striped bass preferred 40-mm gizzard shad when exposed to small prey, a preference that weakened when these small predators preyed on intermediately sized gizzard shad. Large hybrid striped bass did not prefer any single gizzard shad size across all three size combinations. In fact, both large and small hybrid striped bass consumed prey as large as their mouth gape without reduced capture efficiency.

In the field, piscivores consume smaller prey than predicted by optimality considerations (Juanes 1994). Hybrid striped bass from West Point Reservoir rarely consumed gizzard shad > 65 mm, despite being capable of consuming these larger prey (Ott and Malvestuto 1981). In short-term pond experiments, hybrid striped bass also ate smaller gizzard shad than were available (Dettmers et al., in press). In my view, these patterns cannot be explained by reduced capture efficiency as prey size approaches piscivore gape constraints. Rather, they appear to derive from interactions between piscivore and prey that operate at larger spatial scales than my observation chamber.

Vulnerability can be reduced through habitat choice, schooling, and escape responses (Savino and Stein 1982; Pitcher 1986; Christensen and Persson 1993). Spatial overlap among piscivores and prey mediated by temperature
and dissolved oxygen preferences (Coutant 1985), as well as reduced piscivore search efficiency under highly turbid conditions also can reduce prey susceptibility (Miner 1990; Miner and Stein, in press) and may cause piscivores to consume only small, vulnerable prey. Finally, because age-0 gizzard shad are the most abundant fish in Ohio reservoirs during summer and fall (Johnson 1986), hybrid striped bass are simply more likely to encounter these small prey.

Putting my behavioral insights into a food web context, I suggest that, despite no hybrid striped bass size selection in the laboratory, other processes frequently constrain hybrid striped bass to consume gizzard shad < 60 mm. Hence, if hybrid striped bass primarily eat gizzard shad < 60 mm, they should consume large numbers of those gizzard shad most likely to suppress zooplankton, providing an opportunity to increase zooplankton abundance. In reservoirs, gizzard shad < 60 mm regulate spring and summer zooplankton populations (Dettmers and Stein 1992; DeVries and Stein 1992; Yako et al. submitted).

The success of hybrid striped bass in regulating gizzard shad depends on system productivity and timing issues. To improve sport-fish recruitment, zooplankton enhancement must occur when sport fishes are zooplanktivorous in the limnetic zone. Based on my previous work, zooplankton may be maintained at 100·L⁻¹ only if age-0 gizzard shad are < 10·m⁻³ and crustacean zooplankton production exceeds 220 mg·m⁻³·d⁻¹.
(Dettmers et al., in press). Any piscivore must reduce age-0 gizzard shad to < 10·m$^{-3}$ to permit zooplankton to persist at 100·L$^{-1}$ by mid-July for late-hatching sport fishes (DeVries et al. 1991). Thus, hybrid striped bass have the potential to improve sport-fish recruitment only in the most productive reservoirs.

Bioenergetics simulations revealed that abundant hybrid striped bass may hasten the age-0 gizzard shad decline by as much as four weeks. However, if gizzard shad abundance initially exceeds 25·m$^{-3}$, reductions to 10 gizzard shad·m$^{-3}$ may not be realized until August or later, too late in the season for increased zooplankton to improve sport-fish recruitment, regardless of productivity. Further, when initial gizzard shad abundance was 15-25·m$^{-3}$, only stocking hybrid striped bass at densities higher than management agencies typically stock these piscivores (Crandall 1978; Morris and Follis 1978; Ott and Malvestuto 1981; Jahn et al. 1987) caused gizzard shad declines before mid-July.

These predictive scenarios are subject to uncertainty. I have not directly estimated mortality for age-0 gizzard shad. However, my modeling scenarios do reflect the suite of outcomes I might expect from low to high natural mortality of gizzard shad. When age-0 gizzard shad abundance was 38·m$^{-3}$ and natural mortality was low (99%), hybrid striped bass had little overall impact on the population. If mortality is less than 99%, piscivores will
have an even smaller impact. Conversely, my scenario with low gizzard shad abundance and high natural mortality of age-0 gizzard shad (99.99%) revealed that age-0 gizzard shad fell below 10 m$^{-3}$ by July 1, before hybrid striped bass consumption could alter gizzard shad mortality patterns and potentially increase zooplankton.

My model predictions are consistent with previous bioenergetics modeling efforts to explore how piscivore consumption might affect gizzard shad populations. In a generalized Ohio reservoir, a dense largemouth bass Micropterus salmoides population (33.4 kg·ha$^{-1}$) consumed the entire annual gizzard shad production only when age-0 gizzard shad abundance was low due to poor recruitment (Carline et al. 1984). When age-0 recruitment was high, largemouth bass consumed < 60% of annual production.

In Kokosing Reservoir, Ohio, stocked esocids and percids, plus resident largemouth bass consumed only 20% of age-0 gizzard shad production (Johnson et al. 1988) when stocked at a combined density of 170 fish·ha$^{-1}$ and resident largemouth bass biomass was only 4.5 kg·ha$^{-1}$. When hybrid striped bass biomass was about 8 kg·ha$^{-1}$, gizzard shad populations were unaffected unless density was low and natural mortality was high. Conversely, when hybrid striped bass are stocked to achieve densities of 22-32 kg·ha$^{-1}$, similar to the piscivore density of Carline et al. (1984), age-0 gizzard shad reductions can occur.
However, even these gizzard shad reductions are unlikely to improve sport-fish recruitment because 1) < 10% of Ohio reservoirs are likely to exhibit age-0 gizzard shad densities < 10·m−3 and zooplankton production exceeding 220 mg·m−3·d−1 (Dettmers et al., in press), 2) hybrid striped bass do not reduce age-0 gizzard shad to near 10·m−3 until after August 1 if initial density exceeds 15·m−3 and natural mortality is < 99.99%, 3) the density of hybrid striped bass required to cause such gizzard shad reductions would be 3 to 4 times the usual rate of stocking for these piscivores. Most often this reduction occurs after August 1, too late for increased zooplankton to improve sport-fish recruitment. Thus, in shallow, turbid, eutrophic reservoirs similar to systems in Ohio, I expect that hybrid striped bass would be unlikely to improve sport fish recruitment.
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Table 9. Summary of the experimental design used for laboratory size-selection experiments. *N* refers to the number of hybrid striped bass used for each treatment. Each piscivore was given at least three trials within a treatment.

<table>
<thead>
<tr>
<th>Piscivore length (TL, mm)</th>
<th>N</th>
<th>Gizzard shad combination</th>
<th>Gizzard shad lengths (TL, mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>190-250</td>
<td>5</td>
<td>Small</td>
<td>40, 60, 80</td>
</tr>
<tr>
<td>190-250</td>
<td>3</td>
<td>Intermediate</td>
<td>60, 80, 100</td>
</tr>
<tr>
<td>190-250</td>
<td>0</td>
<td>Large</td>
<td>80, 100, 120</td>
</tr>
<tr>
<td>310-360</td>
<td>1</td>
<td>Small</td>
<td>40, 60, 80</td>
</tr>
<tr>
<td>310-360</td>
<td>3</td>
<td>Intermediate</td>
<td>60, 80, 100</td>
</tr>
<tr>
<td>310-360</td>
<td>1</td>
<td>Large</td>
<td>80, 100, 120</td>
</tr>
</tbody>
</table>
Table 10. Growth and P-value (the proportion of maximum consumption required to achieve observed growth) of each modeled hybrid striped bass cohort. P-values were calculated with the bioenergetics model using empirical growth estimates from Austin and Hurley (1987).

<table>
<thead>
<tr>
<th>Hybrid striped bass cohort</th>
<th>Annual growth (g wet weight)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age-0</td>
<td>0.4 - 13</td>
<td>1.11</td>
</tr>
<tr>
<td>Age-1</td>
<td>13.0 - 503</td>
<td>0.82</td>
</tr>
<tr>
<td>Age-2</td>
<td>503.0 - 1778</td>
<td>0.61</td>
</tr>
</tbody>
</table>
Table 11. Distribution of peak larval gizzard shad densities across reservoir-years. This data set comprises 48 reservoir-years from 18 Ohio reservoirs sampled in as many as 5 years. I am indebted to D. R. DeVries, J. G. Miner, M. T. Bremigan, T. P. Stahl, J. G. Garvey, and N. S. Donovan for their efforts to collect this data and kind permission to publish this table.

<table>
<thead>
<tr>
<th>Peak larval gizzard shad density (number·m⁻³)</th>
<th>Frequency of occurrence</th>
<th>Proportion of reservoir-years</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-5</td>
<td>13</td>
<td>0.27</td>
</tr>
<tr>
<td>6-10</td>
<td>6</td>
<td>0.13</td>
</tr>
<tr>
<td>11-15</td>
<td>6</td>
<td>0.13</td>
</tr>
<tr>
<td>16-20</td>
<td>6</td>
<td>0.13</td>
</tr>
<tr>
<td>21-25</td>
<td>5</td>
<td>0.10</td>
</tr>
<tr>
<td>26-30</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>31-35</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>36-40</td>
<td>5</td>
<td>0.10</td>
</tr>
<tr>
<td>&gt;41</td>
<td>6</td>
<td>0.13</td>
</tr>
</tbody>
</table>
Figure 16. Proportion of gizzard shad size classes eaten by all small (A) and large (B) hybrid striped bass when feeding on each gizzard shad length combination in a laboratory. N is the number of piscivores tested for each combination; n is the sum of the trials run by N piscivores for each combination. Small, intermediate, and large refer to gizzard shad size as described in Table 9.
Figure 16

A. Small Hybrid Striped Bass
(190-250 mm)

N = 5
n = 18

N = 3
n = 10

B. Large Hybrid Striped Bass
(310-360 mm)

N = 1
n = 4

N = 3
n = 9

N = 1
n = 5

Proportion Eaten by Hybrid Striped Bass

Small Interm ediate Large
Gizzard Shad Length Combinations

N = Number of fish
n = Number of trials
Figure 17. Capture efficiency (± 1 SE) of small (A) and large (B) hybrid striped bass when feeding on each gizzard shad length combination. N is the number of piscivores used with each combination. Small, intermediate, and large refer to gizzard shad length combinations as described in Table 9.
A. Small Hybrid Striped Bass
(190-250 mm)
N = 5
N = 3

B. Large Hybrid Striped Bass
(310-360 mm)
N = 1
N = 1

Capture Efficiency of Hybrid Striped Bass

Small Intermediate Large
Gizzard Shad Length Combinations

Figure 17
Figure 18. Small (A) and large (B) hybrid striped bass capture efficiency plotted against ratio of prey body depth to piscivore mouth gape. Note that their capture efficiency remained high as this ratio approached 1, suggesting that hybrid striped bass capture efficiency was not limited by prey body depth.
Capture Efficiency (Captures per Attack)

Gizzard Shad Body Depth

Hybrid Striped Bass Mouth Gape

Figure 18
Figure 19. Lakewide age-0 gizzard shad abundance during May 15-December 31, assuming a natural gizzard shad mortality of 99% and initial abundance of 15·m⁻³ (A), 25·m⁻³ (B), or 38·m⁻³ (C). I then predicted the shift in age-0 gizzard shad abundance caused by consumption by hybrid striped bass stocked to achieve densities of 8, 22, and 32 kg·ha⁻¹. The horizontal dashed line represents a gizzard shad abundance that corresponds to 10 individuals·m⁻³.
Figure 19
Figure 20. Lakewide age-0 gizzard shad abundance during May 15-December 31, assuming a natural gizzard shad mortality of 99.99% and initial abundance of 15·m⁻³ (A), 25·m⁻³ (B), or 38·m⁻³ (C). I then predicted the shift in age-0 gizzard shad abundance caused by consumption by hybrid striped bass stocked to achieve densities of 8, 22, and 32 kg·ha⁻¹. The horizontal dashed line represents a gizzard shad abundance that corresponds to 10 individuals·m⁻³.
A. 15 Gizzard Shad m$^{-3}$

B. 25 Gizzard Shad m$^{-3}$

C. 38 Gizzard Shad m$^{-3}$

Lakewide Gizzard Shad Abundance

July 1  Sept. 1  Nov. 1  December 31

Date

Figure 20
CHAPTER VI
CONCLUSIONS

Reservoir food webs are regulated through both top-down and bottom-up mechanisms that appear less tightly coupled than those of north temperate lakes. Because gizzard shad reaches high densities in reservoirs (Summers and Axon 1979; Filipek 1980; Orth 1980; Willis and Jones 1986), it exerts strong top-down effects on zooplankton, especially during early life stages (DeVries and Stein 1992; Dettmers and Stein 1992). As an omnivore >30 mm TL, gizzard shad can eliminate zooplankton, then switch to phytoplankton and detritus (Miller 1960; Bodola 1966). By eliminating zooplankton, gizzard shad may compromise recruitment of planktivorous sport fishes (e.g., bluegill) and may reduce survival of age-0 largemouth bass through indirect effects (DeVries et al. 1991; Stein et al. in press). Piscivores potentially can control gizzard shad, reducing its abundance, permitting increased zooplankton, and potentially improving sport-fish recruitment. My dissertation begins to address these issues.

Though omnivorous, age-0 gizzard shad consume more zooplankton if more is available to them but overall they
consume less zooplankton as they grow larger, i.e., from 30 to 60 mm (Chapter II). Though gizzard shad consume less zooplankton as they grow, they retain their ability to use zooplankton, consuming more if more is available. Hence, large gizzard shad > 30 mm as well as small ones < 30 mm may play important roles in regulating reservoir zooplankton.

Given the apparent keystone status of age-0 gizzard shad in reservoirs, I experimentally examined the potential for piscivores to reduce gizzard shad in 0.4-ha ponds and permit increased zooplankton (Chapter III). I documented a trophic cascade from piscivores to zooplankton. Hybrid striped bass reduced age-0 gizzard shad immediately upon their addition, permitting zooplankton to persist above 100·L⁻¹ throughout the experiment in my piscivore treatment. This sort of top-down cascade likely will occur in Ohio reservoirs only about when age-0 gizzard shad abundance is < 10·m⁻³ and zooplankton production exceeds 220 mg·m⁻³·d⁻¹.

My experiments in Chapter IV begin to quantify the conditions under which zooplankton can be expected to persist at > 100·L⁻¹, a density appropriate for obligate zooplanktivorous larval fishes. In the face of age-0 gizzard shad consumption, zooplankton persistence was affected by zooplankton production. Zooplankton were eliminated from enclosures when gizzard shad were present, regardless of density if zooplankton production was intermediate to low and were eliminated if age-0 gizzard
shad density was > 12·m\(^{-3}\) when zooplankton productivity was high. Across both 1-m\(^3\) enclosures and 0.4-ha ponds, zooplankton persisted above 100·L\(^{-1}\) if age-0 gizzard shad were < 10·m\(^{-1}\). Phytoplankton biovolume dynamics were decoupled from higher trophic levels unless *Daphnia* were abundant.

In Chapter V, I explored size selection by hybrid striped bass and then used this information in a bioenergetics model to quantify whether these piscivores reduce gizzard shad with resultant increased zooplankton at a time when planktivorous life stages of sport fishes occur in reservoirs. Hybrid striped bass can feed on age-0 gizzard shad during the entire growing season because they exhibit no selection of gizzard shad based on size in laboratory experiments. When age-0 gizzard shad abundance is > 15·m\(^{-1}\), my hybrid striped bass bioenergetics model predicted that these piscivores can reduce gizzard shad to < 10·m\(^{-1}\) up to four weeks earlier than just natural mortality. However, this reduction occurred only after August 1 when natural mortality was low and well after disappearance of sport fishes from the open water.

**Management Implications**

Managing reservoirs to increase zooplankton abundance, so as to increase survival of sport fishes with obligate zooplanktivorous larvae, has the potential for success only in about 5% of Ohio reservoirs. This low potential derives
from frequently abundant age-0 gizzard shad coupled with zooplankton production < 220 mg·m⁻³·d⁻¹. Similarly, managers are unlikely to realize improved water clarity in reservoirs because 1) most zooplankton are small-bodied forms that cannot exert sufficient grazing pressure on phytoplankton and 2) much of Ohio reservoir turbidity is inorganically rather than organically based (Stein et al., in press).

Hybrid striped bass can increase zooplankton, but their effects are subject to tremendous variability in gizzard shad abundances coupled with the capacity of management agencies to stock them at very dense levels for multiple consecutive years and restrict harvest of these piscivores. As a result, managers may be unwilling to devote a large proportion of their hatchery production to only a few reservoirs. As an alternative to stocking hybrid striped bass for biomanipulation, managers likely can generate excellent sport fisheries by stocking piscivores at lower densities in systems with abundant gizzard shad. Thus, managers can stock piscivores simply to improve recreational fishing without generating false hope for more widespread improvements in reservoir communities.
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APPENDIX
Table 12. Seasonal diet composition of three cohorts of hybrid striped bass summarized from Austin and Hurley (1987). Fish eaten by hybrid striped bass were assumed to be gizzard shad. Zooplankton consisted of copepods, *Alona*, *Bosmina*, *Chydorus*, *Daphnia*, *Diaphanosoma*, and *Leptodora*; benthos consisted of Dipterans, corixids, and crayfish.

<table>
<thead>
<tr>
<th>Hybrid striped bass cohort</th>
<th>Food Taxon</th>
<th>April-June</th>
<th>July-September</th>
<th>October-December</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age-0</td>
<td>Zooplankton</td>
<td>80</td>
<td>80</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>Benthos</td>
<td>15</td>
<td>15</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>5</td>
<td>5</td>
<td>20</td>
</tr>
<tr>
<td>Age-1</td>
<td>Zooplankton</td>
<td>15</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Benthos</td>
<td>25</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>60</td>
<td>90</td>
<td>90</td>
</tr>
<tr>
<td>Age-2</td>
<td>Zooplankton</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Benthos</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Fish</td>
<td>95</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>
Table 13. Number of age-0 gizzard shad consumed by three cohorts of hybrid striped bass stocked at three different densities during 30-d intervals during May 15-December 31. Gizzard shad lengths through time represent mean lengths collected by electrofishing (JMD, unpublished data).

<table>
<thead>
<tr>
<th>Interval</th>
<th>Gizzard shad length (mm)</th>
<th>Number of gizzard shad consumed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>125·ha⁻¹</td>
</tr>
<tr>
<td>June 1-14</td>
<td>20</td>
<td>7.16 x 10³</td>
</tr>
<tr>
<td>July 1-31</td>
<td>35</td>
<td>1.91 x 10⁵</td>
</tr>
<tr>
<td>August 1-31</td>
<td>45</td>
<td>8.40 x 10⁴</td>
</tr>
<tr>
<td>September 1-31</td>
<td>60</td>
<td>4.56 x 10⁴</td>
</tr>
<tr>
<td>October 1-31</td>
<td>75</td>
<td>3.48 x 10⁴</td>
</tr>
<tr>
<td>November 1-31</td>
<td>80</td>
<td>1.59 x 10⁴</td>
</tr>
<tr>
<td>December 1-31</td>
<td>80</td>
<td>1.35 x 10³</td>
</tr>
</tbody>
</table>