EFFECTS OF ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) INVASION ON THE AQUATIC COMMUNITY OF A GREAT PLAINS RESERVOIR

by

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Abstract

The zebra mussel is an invasive bivalve that was first confirmed in Kansas in 2003, and has decreased zooplankton abundance and altered the aquatic community in other areas where it has invaded. However, little is known about its effects on the aquatic communities of warm-water Great Plains reservoirs. We analyzed zooplankton, benthic macroinvertebrate, and juvenile and small-bodied fish abundance in the littoral zone of an Eastern Kansas reservoir with an established zebra mussel population (El Dorado Reservoir) and a control reservoir without zebra mussels (Melvern Reservoir) for two years pre-zebra mussel invasion (2001-2002) and two years post-invasion (2008-2009). We found no difference in littoral zooplankton abundance between reservoirs across time, but abundance of some macroinvertebrate taxa increased, and abundance of juvenile *Lepomis* spp. and red shiners decreased in the littoral zone of El Dorado Reservoir in August of the post-zebra mussel invasion period in comparison to the control reservoir. We also analyzed abundance and condition of six adult reservoir fishes in El Dorado Reservoir and three control reservoirs in Eastern Kansas for ten years pre-zebra mussel invasion (1993-2002) and five years post-invasion (2004-2008). Adult white crappie abundance remained constant in El Dorado Reservoir but decreased in the control reservoirs during the post-zebra mussel invasion period, and condition of adult bluegill, white bass, and white crappie decreased in El Dorado Reservoir in the post-zebra mussel invasion period compared to the control reservoirs. Our findings suggest that zebra mussel invasion in El Dorado Reservoir may have affected some benthic macroinvertebrates, juvenile and small-bodied fishes, and adult fishes. We did not find evidence that zebra mussels have had substantial effects on the zooplankton community

of El Dorado Reservoir. However, July-August zebra mussel veliger densities in El Dorado Reservoir averaged less than 12 veligers/L in four of the six post-zebra mussel invasion years. Additional research and long-term monitoring of zooplankton, macroinvertebrates, and fishes will be necessary to determine the full effects of zebra mussels on the aquatic communities of warm-water reservoirs throughout North America.

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Dedication

This thesis is dedicated to my father, Steven Severson, who has shared his love and knowledge of fisheries with me since my childhood. I also dedicate this thesis to my mother, Cindy Severson, and my husband, Joshua Christianson—this thesis would have not been possible without your love, support, and encouragement. Thank you.

Preface

Though I am the primary author of this thesis, it has been formatted for submission for publication as a work by multiple authors.

CHAPTER 1 - Effects of zebra mussel invasion on the littoral community of El Dorado Reservoir

Introduction

The effects of biological invasions can be both ecologically and economically costly (Lockwood et al. 2007). There are an estimated 50,000 invasive species in the United States, including thousands of plants, arthropods, and microbes, and hundreds of birds, fish, mollusks, reptiles, amphibians, and mammals (Pimentel et al. 2005). The combined economic impacts of these species are estimated at over $100 billion each year, including agricultural, commercial, and recreational losses, infrastructure damage, and the costs of controlling invasive species to prevent additional damage (Pimentel et al. 2005). In addition, invasive species have been implicated in the decline of nearly half of the species currently listed as federally threatened or endangered (Pimentel et al. 2005).

The zebra mussel (*Dreissena polymorpha*) is an invasive species that was first confirmed in North America in the 1980s, and was predicted to cause billions of dollars of economic losses in the Great Lakes, as well as ecological effects ranging from the disruption of walleye spawning from substrate alteration to the collapse of aquatic food webs and native mussel populations (Roberts 1990; Strayer 2009). The zebra mussel exhibits several traits of a successful invader: prolific reproduction, an easily-transported planktonic (veliger) life stage, byssal threads that allow the mussel to attach to a variety of solid substrates, a relative absence of natural predators outside Eurasia, and a broad environmental tolerance (Ludyanskiy et al. 1993; Ram and McMahon 1996). Zebra mussels have spread throughout much of the Midwestern United States, including the

Great Lakes and the mainstem and tributaries of the Mississippi River (US Geological Survey 2010). Although zebra mussels have invaded North American aquatic ecosystems for over twenty years, numerous questions remain regarding the ecological effects of their invasion.

Zebra mussels may have substantial effects on the lower trophic levels of invaded systems. Zebra mussels are filter-feeding bivalves that consume primarily phytoplankton, but are also known to consume rotifers and other microzooplankton (Horgan and Mills 1997; Wong et al. 2003). Phytoplankton is also a primary diet component for many grazing zooplankton taxa, and a reduction in phytoplankton abundance may impact these taxa (Strayer et al. 1999; Raikow 2004). Several studies have documented a decrease in phytoplankton biomass in the presence of zebra mussels (Caraco et al. 1997; Richardson and Bartsch 1997; Idrisi et al. 2001; Barbiero et al. 2006; Miller and Watzin 2007). However, findings related to zooplankton abundance are less consistent. In Oneida Lake, New York, there was no change in biomass of total zooplankton or macrozooplankton following zebra mussel invasion (Mayer et al. 2000; Idrisi et al. 2001). In contrast, total zooplankton abundance, biomass, and microzooplankton abundance declined in western Lake Erie and the Hudson River following zebra mussel establishment, but the response of cladocerans and copepods (macrozooplankton taxa) was highly variable (MacIsaac et al. 1995; Pace et al. 1998). Mesocosm and *in situ* enclosure experiments have also demonstrated a decrease in the abundance of zooplankton taxa in the presence of zebra mussels (Richardson and Bartsch 1997; Jack and Thorp 2000; Raikow 2004; Miller and Watzin 2007).

Zebra mussels may also affect macroinvertebrate abundance in invaded systems. Zebra mussels release excess or undesirable filtered particles as pseudofecal pellets, in addition to fecal material that is deposited into the sediment. This material may provide additional shelter and food for benthos (MacIsaac 1996; Stewart et al. 1998). In addition, zebra mussels attached to substrate may increase benthic habitat surface area and heterogeneity (Stewart et al. 1998; Horvath et al. 1999). Zebra mussel presence may lead to increased macroinvertebrate abundance, including increased amphipods, chironomids, oligochaetes, and other macroinvertebrate taxa (Karatayev et al. 1997; Ricciardi et al. 1997; Stewart et al. 1998; Beekey et al. 2004). Other taxa have exhibited less consistent responses, but may increase, decrease, or have no change in abundance following zebra mussel invasion (Ricciardi et al. 1997; Stewart et al. 1998; Horvath et al. 1999; Beekey et al. 2004). Increased abundance of macroinvertebrates including amphipods, chironomids, and oligochaetes may lead to altered macroinvertebrate community composition, including altered taxonomic richness (Ricciardi et al. 1997; Horvath et al. 1999; Beekey et al. 2004).

Reductions in zooplankton abundance by zebra mussels, either directly by predation or indirectly by competition, may impact fish species that are planktivorous as adults, or that utilize zooplankton as a primary food source in their larval stages (MacIsaac 1996; Trometer and Busch 1999; Raikow 2004; Pothoven and Madenjian 2008). Decreased food availability may lead to reductions in growth and abundance of fishes, and may decrease age-0 fish survival (Trometer and Busch 1999; Raikow 2004). However, the effects of zebra mussel invasion on growth and abundance of fishes have been mixed. Age-0 yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), freshwater drum (*Aplodinotus grunniens*), gizzard shad (*Dorosoma cepedianum*), and white bass (*Morone chrysops*) exhibited no difference in growth before and after zebra mussel invasion in the Western Basin of Lake Erie (Trometer and Busch 1999). Similarly, growth of age-0 bluegill (*Lepomis macrochirus*) did not differ between mesocosms with and without zebra mussels (Richardson and Bartsch 1997), and yellow perch growth in Oneida Lake, New York (Mayer et al. 2000; Idrisi et al. 2001) did not differ before and after zebra mussel invasion. In contrast, white perch (*Morone americana*), American shad (*Alosa sapidissima*), alewife (*Alosa pseudoharengus*), striped bass (*Morone saxatilis*), and blueback herring (*Alosa aestivalis*) in the Hudson River estuary exhibited decreases in apparent growth or abundance following zebra mussel invasion (Strayer et al. 2004), but yellow perch abundance increased after zebra mussel invasion in Western Lake Erie (Trometer and Busch 1997).

Most studies examining the ecological effects of zebra mussel have focused on the cool- to cold-water environments of the Great Lakes region, and may have limited applicability to the turbid, warm-water systems typical of the Great Plains and the Southern United States, where summer water temperatures and turbidity may exceed the optimal ranges of the zebra mussel (17-23° C, 40-200 cm Secchi disc; Ludyanskiy et al. 1993). Our objectives were to determine if littoral zone zooplankton, benthic macroinvertebrate, and fish populations in a Great Plains reservoir changed following zebra mussel invasion. We tested the hypothesis that littoral zone microzooplankton, macrozooplankton, and total zooplankton abundance would decline following zebra mussel invasion, and that these declines would impact zooplankton community composition. We also tested the hypothesis that benthic macroinvertebrates, especially

Amphipoda, Chironomidae, and Oligochaeta, would increase in abundance in the littoral zone following invasion and consequently alter community composition (Karatayev et al. 1997; Ricciardi et al. 1997; Stewart et al. 1998). Finally, we tested the hypothesis that the abundance of juvenile and adult small-bodied fish, as well as the growth of age-0 largemouth bass (*Micropterus salmoides*), would decline in the littoral zone following zebra mussel invasion.

Site Description

El Dorado and Melvern reservoirs are large federal reservoirs designed for flood control and water resource development in eastern Kansas. Both reservoirs are located in watersheds composed primarily of prairie and cropland. El Dorado Reservoir has a surface area of 3,237 ha and a mean depth of 3.3 m; Melvern Reservoir has a surface area of 2,833 ha and a mean depth of 6.1 m. Mean summer water temperature in both reservoirs ranged between 27-32° C, mean summer dissolved oxygen ranged between 4-8 mg/L, and mean turbidity ranged between 6-206 NTU. In addition, vegetation cover in the littoral zone of both reservoirs ranged from 0-50 stems/m^2 during the study period (See Appendix A.1). Both reservoirs host sportfish communities including *Micropterus* spp., *Lepomis* spp., *Morone* spp., walleye, white crappie (*Pomoxis annularis*), and ictalurids. Gizzard shad are a primary forage fish, but cyprinids and *Percina* spp. were also found in the reservoirs (Tripe 2000; Schultz et al. 2002; Kansas Department of Wildlife and Parks 2010a, 2010b). Zebra mussels were confirmed in Kansas in El Dorado Reservoir in 2003, with average July-August zebra mussel veliger densities of less than 12 veligers/L for four out of the six post-invasion years (2004-2009) and densities of less than 2 veligers/L in 2008-2009, while Melvern Reservoir has remained free of zebra mussels (J. Goeckler, Kansas Department of Wildlife and Parks, unpublished data).

Methods

Fieldwork and Laboratory Methods

Sampling of fish, zooplankton, and macroinvertebrates was conducted in July and August at El Dorado and Melvern reservoirs for two years prior to confirmed zebra mussel establishment (2001-2002) and two years following zebra mussel establishment (2008-2009). Sampling was conducted within six randomly selected coves per reservoir per month (Strakosh et al. 2009). Two 24.5-m by 6.1-m transects parallel to the shoreline in each cove were randomly selected for sampling each month. Each transect was sampled a maximum of once per sampling year. Transects sampled in 2001-2002 were enclosed before sampling using a 3.2-mm bar-mesh block net 2.0-m high by 30.6-m long. The block net was omitted from sampling in 2008 and 2009 because Schoenebeck et al. (2005) indicated no difference in fish sampling efficiency between enclosed and unenclosed areas.

Zooplankton were sampled 3.1-m and 6.1-m from shore using a 63-µm mesh tow net (20-cm diameter) pulled parallel to the shoreline for the length of each transect (24.5 m). Samples were preserved with 10% buffered neutral formalin. In the laboratory, each sample was randomly subsampled three times; zooplankton in each subsample were identified to family and enumerated. Number of zooplankton per liter (n/L) was calculated for each sample by taxonomic group. Macroinvertebrates were sampled at six locations within the transect (8.2 and 16.2 m from the left side of the enclosure, and sampling at 2, 4, and 6 m from shoreline) using a 500-µm D-frame net (30-cm by 25-cm) with an attached dolphin bucket. The net was swiped along substrate and vegetation for 0.25-m; collected invertebrates and debris were preserved in 10% formalin with rose bengal dye (100 mg/L; Toczydlowski 1984). Macroinvertebrates were sorted in the laboratory, identified to family, and enumerated; number of invertebrates per enclosure (n/E) was calculated for each taxonomic group by summing total invertebrates from all six samples per enclosure.

Each transect was electrofished with a Smith-Root LR-24 backpack electrofishing unit (2008-2009), or a Smith-Root 15-C backpack electrofishing unit (2001-2002) using 200-300 volts pulsed DC at 30-60 Hz and 12-48% duty cycle. The transect was sampled in a zigzag pattern by two individuals, one shocking and netting and the other netting (Strakosh et al. 2009). Species that were easily identified in the field other than *Lepomis* or *Micropterus* spp., as well as any fish greater than 200 mm (*Lepomis* and *Micropterus* spp. included), were measured (total length), enumerated, and released. All other fish were frozen and returned to the laboratory to be identified to species, enumerated, and measured. Sagittal otoliths were removed from age-0 largemouth bass, mounted on glass slides, polished, and examined for daily growth rings. Two individuals examined and recorded daily rings independently of each other; the two daily growth ring counts were averaged together and five days were added to the average value to account for age at swim-up (Strakosh et al. 2009). Otoliths with count discrepancies of more than seven days were recounted independently a second time by the same observers. If a discrepancy remained, the otolith was omitted from sample. Growth was calculated as mm/day (Tripe 2000; Strakosh et al. 2009).

Statistical Methods

A nested analysis of variance (ANOVA; coves nested within reservoirs) with interactions was used to determine whether mean zooplankton abundance (n/L) or mean macroinvertebrate abundance (n/E) differed following zebra mussel invasion. Linear orthogonal contrasts were used to test the null hypothesis that there was no difference between reservoirs (invaded and control) or time periods (pre- and post-zebra mussel invasion) for each month (July and August). We analyzed zooplankton abundance by three groups: mean total zooplankton, mean microzooplankton (nauplii and rotifers), and mean macrozooplankton (cladocerans *Bosmina*, *Chydorus*, *Daphnia*, *Holopedium*, *Leptodora*, and *Sida*; calanoid, cyclopoid, harpacticoid, and poecilostomatoid copepods; ostracods) (Pace 1986; Strayer et al. 1999; Raikow 2004; Miller and Watzin 2007). We analyzed macroinvertebrate abundance by four groups: mean total benthic macroinvertebrates, mean Amphipoda, mean Chironomidae, and mean Oligochaeta (Karatayev et al. 1997; Ricciardi et al. 1997; Stewart et al. 1998; Beekey et al. 2004).

Mean zooplankton and macroinvertebrate taxonomic richness, Simpson's diversity index, and evenness based on Simpson's diversity index were also analyzed by month using a nested ANOVA with contrasts and interactions to determine whether there was a shift in the zooplankton or macroinvertebrate community in response to zebra mussel invasion. Samples with evenness values greater than one (28 total zooplankton samples) were excluded from statistical analyses of evenness; these values appeared to be an artifact of rounding error and low taxonomic richness. Simpson's diversity index values range from zero to one; the closer the index value was to one, the greater the probability that two randomly sampled organisms from a location were different taxa (Kwak and Peterson 2007). Simpson's diversity index (1 – D) and evenness based on

Simpson's diversity index were both calculated according to Kwak and Peterson (2007). We also used a discriminant analysis to further examine effects of zebra mussel invasion on the zooplankton and macroinvertebrate community. All abundance data for the discriminant analyses were log-transformed to better meet the assumptions of normality. We tested whether the zooplankton or macroinvertebrate community differed among four groups: El Dorado Reservoir pre-invasion, Melvern Reservoir pre-invasion, Melvern Reservoir post-invasion, and El Dorado Reservoir post-invasion separately for both July and August.

Nested ANOVAs with contrasts and interactions were also used to test if juvenile and adult small-bodied fish abundance declined in the littoral zone following zebra mussel invasion. Mean catch per unit effort (CPUE; fish per minute) was used as an index of fish abundance. Only abundance of fish taxa representing at least five percent of the total catch were analyzed, with the exception of largemouth bass and gizzard shad. Largemouth bass are an economically important sport fish and gizzard shad are an important forage fish, and therefore were retained for analysis. *Lepomis* spp. (bluegill, green sunfish *Lepomis cyanellus*, longear sunfish *Lepomis megalotis*, hybrid sunfish, and unidentifiable age-0 *Lepomis* spp.) were grouped together for analysis, as were darters (johnny darter *Etheostoma nigrum*, orangethroat darter *Etheostoma spectabile*, logperch *Percina caprodes*, and slenderhead darter *Percina phoxocephala*). A discriminant analysis was also used to examine the effects of zebra mussel invasion on the littoral fish community. All abundance data for the discriminant analysis were log-transformed to better meet normality assumptions. We tested whether the fish community differed among El Dorado Reservoir pre-invasion, El Dorado Reservoir post-invasion, Melvern Reservoir pre-invasion, and Melvern Reservoir post-invasion.

We used a nested analysis of covariance (ANCOVA; month as covariate) with interactions and orthogonal contrasts to test whether growth of age-0 largemouth bass (mm/day) declined following zebra mussel invasion. All nested ANOVAs and ANCOVAs followed a before-after control-impact (BACI) design, with time period (pre- and post-invasion) and reservoir (invaded and control) as effects. A contrast P-value less than 0.05 was considered significant for all analyses, indicating that trends in abundance, growth, or community indices differed between the two reservoirs over time; all analyses were completed with SAS 9.1.3 (SAS Institute Inc., Cary, North Carolina).

Results

Zooplankton

Zooplankton samples were collected from twelve coves in El Dorado and Melvern reservoirs from 2001 to 2009 (90 samples in July, 83 samples in August; 77 samples pre-invasion, 96 samples post-invasion). Mean total zooplankton (n/L) ranged from 5.24 (SE = 1.07; Melvern; August 2001) to 38.52 (SE =15.04; El Dorado; July 2001), and was similar between reservoirs across time for both July ($P = 0.460$) and August ($P = 0.845$; Figure 1.1). Mean microzooplankton abundance ranged from 2.55 (SE = 0.18; El Dorado; July 2008) to 24.20 (SE =14.20; El Dorado; July 2001), and was consistent between reservoirs across time for July ($P = 0.336$) and August ($P = 0.638$; Figure 1.1). Mean macrozooplankton abundance ranged from 1.23 (SE = 0.14; Melvern; August 2009) to 19.25 (SE =5.05; Melvern; July 2001) and was similar between reservoirs across time for July ($P = 0.591$) and August ($P = 0.567$; Figure 1.1). Thus, mean zooplankton abundance trends were similar between El Dorado and Melvern reservoirs between the pre- and post-zebra mussel invasion time periods.

Mean zooplankton taxonomic richness (total number of taxa per sample) ranged from 4.13 (SE = 0.14; Melvern; August 2009) to 6.46 (SE = 0.30; El Dorado; July 2008), and did not differ between the reservoirs across time in July (*P* = 0.174). A marginally significant *P*-value in August (*P* = 0.056; Figure 1.2) was due to a steady decline in zooplankton taxonomic richness in Melvern Reservoir, but high among-year variability in El Dorado Reservoir. Mean Simpson's diversity index ranged from 0.50 (SE = 0.02; El Dorado; July 2009) to 0.73 (SE = 0.01; El Dorado; July 2008, August 2009), and did not differ between reservoirs across time for either July (*P* = 0.869) or August (*P* = 0.714; Figure 1.2). Mean taxonomic evenness ranged from 0.65 (SE = 0.03; El Dorado; July 2009) to 0.87 (SE = 0.01; El Dorado; July 2008, August 2008), and did not differ between reservoirs over time in July (*P* = 0.668) or August (*P* = 0.849; Figure 1.2). Thus, mean taxonomic richness, mean Simpson's diversity index, and mean taxonomic evenness was relatively similar between El Dorado and Melvern reservoirs pre- and post-zebra mussel invasion.

The discriminant function analyses of zooplankton abundance revealed substantial overlap in communities before and after zebra mussel invasion for both July and August. The zooplankton community in El Dorado Reservoir in July following zebra mussel invasion tended to have more *Leptodora* than in the pre-invasion period, while pre-invasion samples had greater abundance of calanoid and cyclopoid copepods, nauplii, and *Chydorus*. In addition, pre-invasion samples of Melvern Reservoir zooplankton tended to have higher abundance of *Bosmina*, Cyclopoid copepods, nauplii, and *Chydorus* (Wilks'

Lambda = 0.217; $P < 0.001$). However, 38% of July samples were misclassified, indicating substantial overlap in zooplankton communities (Figure 1.3). In August, both reservoirs had more similar zooplankton communities post-invasion than pre-invasion. El Dorado Reservoir had higher *Daphnia* abundance pre-invasion, and Melvern Reservoir had higher *Bosmina* and *Chydorus* abundance pre-invasion (Wilks' Lambda = 0.062; $P < 0.001$). However, 28% of August samples were misclassified, suggesting no distinct pattern in zooplankton community shifts between the two lakes from the pre- to the post-zebra mussel invasion period (Figure 1.3).

Macroinvertebrates

Benthic macroinvertebrate samples were collected from 12 coves in El Dorado and Melvern reservoirs, with 95 samples collected pre-invasion (2001-2002; 47 in July and 48 in August) and 95 samples collected post-invasion (2008-2009; 48 in July and 47 in August). A total of fifty different taxa were sampled across the entire study period. Mean total benthic macroinvertebrates (n/E) ranged from 0.32 (SE = 0.08; El Dorado; July 2008) to 54.3 (SE = 11.28; Melvern; July 2001), and trends were similar between reservoirs across time in July ($P = 0.929$; Figure 1.4). However, mean total macroinvertebrate abundance in El Dorado Reservoir in August increased from 9.17 (SE = 1.25) pre-invasion to 10.15 (SE = 1.72) post-invasion (11% increase), while abundance in Melvern Reservoir declined from 14.25 (SE = 7.42) to 6.05 (SE = 1.59) during the same time period, but was heavily influenced by high macroinvertebrate abundance in 2001 (58% decline; $P = 0.013$; Figure 1.4). Mean Amphipoda abundance ranged from 0.00 (El Dorado, August 2001-2002; Melvern, August 2008) to 3.26 (SE = 0.98; El Dorado; August 2009). A marginally significant *P*-value in July was due to an increase in mean amphipod abundance in El Dorado from 0.17 (SE = 0.08) pre-invasion to 0.60 (SE = 0.58) post-invasion (253% increase), while mean July amphipod abundance in Melvern decreased from 0.74 (SE = 0.66) pre-invasion to 0.12 (SE = 0.08) post-invasion (84% decline; *P* = 0.053; Figure 1.5). In addition, mean August amphipod abundance in El Dorado Reservoir increased from 0.00 in the pre-invasion period to 1.64 (SE = 1.61) in the post-invasion period, while August amphipod abundance in Melvern Reservoir increased from 0.25 (SE = 0.17) pre-invasion to 0.47 (SE = 0.47) in the post-invasion period (*P* = 0.015; Figure 1.5). Mean Chironomidae abundance ranged from 0.00 (El Dorado, July 2008) to 40.10 (SE = 9.09; Melvern; July 2001), and trends were similar between reservoirs across time in July (*P* = 0.842; Figure 1.5). However, mean August chironomid abundance in El Dorado Reservoir declined from 3.46 (SE = 0.88) pre-invasion to 3.33 (SE = 0.97) post-invasion (4% decline), while abundance in Melvern Reservoir declined from 6.88 (SE = 2.38) to 1.97 (SE = 0.22; 71% decline) in the same time period (*P* = 0.007; Figure 1.5). Mean Oligochaeta abundance ranged from 0.01 (SE = 0.01; El Dorado; July 2008) to 3.79 (SE = 0.58; El Dorado; August 2008), and trends were consistent between reservoirs across time in July (*P* = 0.342; Figure 1.5). However, mean August oligochaete abundance in El Dorado Reservoir increased from 0.42 (SE = 0.25) in the pre-invasion period to 2.40 (SE = 1.40) in the post-invasion period (471% increase), while oligochaete abundance in Melvern Reservoir declined from 0.88 (SE = 0.46) to 0.83 (SE = 0.13) over the same time period (6% decrease; *P* = 0.025; Figure 1.5).

Mean macroinvertebrate taxonomic richness ranged from 0.25 (SE = 0.06; El Dorado; July 2008) to 6.80 (SE = 0.66; Melvern; July 2001), and trends were consistent between reservoirs across time in both July (*P* = 0.983) and August (*P* = 0.143; Figure

1.6). Mean Simpson's diversity index for macroinvertebrate communities ranged from 0.06 (SE = 0.04; El Dorado; July 2008) to 0.59 (SE = 0.02; Melvern; July 2009). Mean July Simpson's diversity index declined from 0.55 (SE = 0.02) pre-invasion to 0.26 (SE = 0.20) post-invasion in El Dorado Reservoir (53% decline), while Simpson's diversity declined from 0.46 (SE = 0.02) to 0.43 (SE = 0.15) during the same time period in Melvern Reservoir (7% decline; $P = 0.001$; Figure 1.6). However, trends in mean Simpson's diversity did not differ between reservoirs across time in August ($P = 0.717$; Figure 1.6). Mean taxonomic evenness ranged from 0.52 (SE = 0.07; Melvern; July2001) to 0.97 (SE = 0.01; Melvern; July 2008), and trends were similar between reservoirs across time in July ($P = 0.126$; Figure 1.6). However, mean August taxonomic evenness declined from 0.88 (SE = 0.06) pre-invasion to 0.81 (SE = 0.01) post-invasion in El Dorado Reservoir (8% decline), while mean evenness increased from 0.77 (SE = 0.01) to 0.85 (SE = 0.02) during the same time period in Melvern Reservoir (10% increase; $P = 0.019$; Figure 1.6).

The discriminant function analyses of benthic macroinvertebrate abundance revealed considerable overlap in communities before and after zebra mussel invasion for both July and August. The macroinvertebrate communities in El Dorado and Melvern Reservoirs in July both tended to have greater abundances of hydrozoans in the post-zebra mussel invasion period than in the pre-invasion period, while pre-invasion samples had greater chironomid abundance. In addition, pre-invasion macroinvertebrate samples from El Dorado Reservoir tended to have higher abundance of Heptageniidae and Ephemeridae mayflies (Wilks' Lambda = 0.034; $P < 0.001$). However, the 57% of samples were misclassified, indicating substantial overlap in the macroinvertebrate communities of El Dorado and Melvern Reservoirs across time (Figure 1.7). August macroinvertebrate samples from the pre- and post-invasion time periods in Melvern Reservoir were relatively similar. In contrast, pre-invasion samples from El Dorado Reservoir in August contained fewer oligochaetes and more Heptageniidae mayflies than samples from the post-zebra mussel invasion period (Wilks' Lambda = 0.033; $P < 0.001$). However, 43% of samples were misclassified, suggesting no distinct pattern in benthic macroinvertebrate community shifts between the two lakes from the pre- to the post-invasion period (Figure 1.7).

Fish Abundance

A total of 6,707 fish were collected in 190 fish samples from 12 coves in El Dorado and Melvern reservoirs, with 95 samples collected in the pre-invasion period (2001-2002; 48 in July and 47 in August) and 95 samples collected in the post-invasion period (2008-2009; 48 in July and 47 in August). Samples contained a total of thirty species but only four species—bluntnose minnow (*Pimephales notatus*), green sunfish, red shiner (*Cyprinella lutrensis*), and western mosquitofish (*Gambusia affinis*)—composed more than five percent of the total abundance (Table 1.1). Western mosquitofish were only sampled in Melvern in 2002, so no further analysis of this species was conducted.

Mean catch per unit effort (CPUE; fish per electrofishing minute) of all fish species combined ranged from 1.06 (SE = 0.24; Melvern; July 2001) to 11.76 (SE = 2.94; El Dorado; August 2002), and was similar between reservoirs in July ($P = 0.382$; Figure 1.8). However, mean total CPUE in August declined from 9.44 (SE = 1.68) pre-zebra mussel invasion to 3.26 (SE = 0.46) post-zebra mussel invasion in El Dorado Reservoir

(65% decline), while mean total CPUE declined from 3.08 (SE = 0.49) pre-invasion to 2.70 (SE = 0.38) post-invasion in Melvern Reservoir (12% decline; $P = 0.007$; Figure 1.8).

Mean bluntnose minnow CPUE ranged from 0.04 (SE = 0.04; El Dorado; August 2009) to 1.45 (SE = 0.52; Melvern; July 2002), and trends in bluntnose minnow abundance were similar between reservoirs across years in July ($P = 0.594$) and August ($P = 0.542$; Figure 1.9). Mean darter CPUE ranged from 0.05 (SE = 0.02; Melvern; July 2001) to 1.02 (SE = 0.44; El Dorado; August 2002), and trends in darter abundance were similar between reservoirs across time for both July ($P = 0.692$) and August ($P = 0.198$; Figure 1.9). Mean gizzard shad CPUE ranged from 0.00 (El Dorado July-August 2008, July 2009; Melvern July-August 2008) to 0.54 (SE = 0.37; El Dorado; July 2002), and trends in gizzard shad abundance were consistent between reservoirs across time for both July ($P = 0.265$) and August ($P = 0.726$; Figure 1.9). Mean *Lepomis* spp. CPUE ranged from 0.17 (SE = 0.04; Melvern; July 2001) to 5.13 (SE = 1.32; El Dorado; August 2002), and trends in *Lepomis* spp. abundance were consistent between reservoirs across years in July (P = 0.266; Figure 1.10). However, mean August CPUE of *Lepomis* spp. declined from 4.29 (SE = 0.85) pre-zebra mussel invasion to 1.65 (SE = 0.33) post-zebra mussel invasion in El Dorado Reservoir (62% decline), while mean CPUE of *Lepomis* spp. in Melvern Reservoir declined from 1.12 (SE = 0.21) to 1.07 (SE = 0.24) during the same time period (4% decline; $P = 0.004$; Figure 1.10). Mean CPUE of largemouth bass (all bass were <120 mm) ranged from 0.00 (El Dorado August 2001, August 2009) to 0.29 (SE = 0.16; Melvern; July 2008), and trends in largemouth bass abundance were similar between reservoirs across time for both July ($P = 0.379$) and August ($P = 0.488$; Figure

1.10). Mean red shiner CPUE ranged from 0.09 (SE = 0.09; Melvern; July 2008) to 1.63 (SE = 0.63; El Dorado; August 2002), and trends in red shiner abundance were similar between reservoirs across years in July ($P = 0.377$; Figure 1.10). However, mean August red shiner CPUE in El Dorado declined from 1.41 (SE = 0.40) pre-zebra mussel invasion to 0.16 (SE = 0.10) post-zebra mussel invasion (88% decline), while Melvern CPUE declined from 0.21 (SE = 0.07) to 0.19 (SE = 0.07) over the same time period (9% decline; $P = 0.039$; Figure 1.10).

The discriminant function analyses of fish abundance in El Dorado and Melvern reservoirs revealed considerable overlap in communities before and after zebra mussel invasion for both July and August. The fish community during the post-zebra mussel invasion period in both El Dorado and Melvern reservoirs in July tended to have fewer red shiners, gizzard shad, and bluntnose minnows than the pre-zebra mussel invasion period. In addition, the fish community in Melvern Reservoir in the post-zebra mussel invasion time period tended to have fewer longnose gar and green sunfish than the pre-zebra mussel invasion period (Wilks' Lambda = 0.029; $P < 0.001$). However, 30% of samples were misclassified, indicating considerable overlap in the fish communities of El Dorado and Melvern Reservoirs across time (Figure 1.11). The fish communities of El Dorado and Melvern Reservoirs in August tended to have more bluegill in the post-invasion period than in the pre-invasion period. In addition, the fish community in Melvern Reservoir during the post-zebra mussel invasion period tended to have fewer bluntnose minnows, largemouth bass, and orangethroat darters than the pre-invasion period. The fish community in El Dorado Reservoir in the post-zebra mussel invasion period contained fewer red shiners, channel catfish, and western mosquitofish than the pre-invasion period (Wilks' Lambda = 0.047; $P < 0.001$). However, 36% of samples were misclassified, suggesting no distinct pattern in fish community shifts between the two lakes from the pre-zebra mussel invasion period to the post-zebra mussel invasion period (Figure 1.11).

Largemouth Bass Growth

A total of 285 age-0 largemouth bass were collected from El Dorado and Melvern reservoirs between July 2001 and August 2009 (164 in July, 121 in August; 211 pre-invasion, 74 post-invasion). No age-0 largemouth bass were collected in El Dorado Reservoir in August 2001 and 2009. Largemouth bass ranged from 28 to 116 mm total length, and mean growth (mm/day) ranged from 0.56 (SE = 0.02; El Dorado 2001) to 0.91 (SE = 0.04; El Dorado 2008). Trends in growth were not consistent between reservoirs across time ($P < 0.001$; Figure 1.12). Mean growth (mm/day) in El Dorado Reservoir increased from 0.74 (SE = 0.01) pre-invasion to 0.88 (SE = 0.03) post-invasion (19% increase), while mean growth in Melvern Reservoir increased from 0.73 (SE = 0.01) pre-invasion to 0.83 (SE = 0.02) post-invasion (14% increase). Thus, mean growth in both reservoirs increased in the post-invasion period, but the magnitude of the increase was greater in El Dorado Reservoir.

Discussion

Our results indicated no changes in zooplankton abundance, zooplankton community composition, or fish community composition following zebra mussel invasion, but did indicate changes in the abundance of some benthic macroinvertebrates, abundance of some fishes, and the growth of age-0 largemouth bass in El Dorado Reservoir. The lack of response of zooplankton in El Dorado Reservoir is likely due to low zebra mussel densities throughout the post-invasion study period in the reservoir. Zebra mussel densities peaked in El Dorado Reservoir in 2006, when the mean July-August veliger density was 148.22/L. In contrast, during July and August of the post-invasion study period (2008-2009) in El Dorado Reservoir, the mean veliger density ranged from 0.26 to 1.02/L (J. Goeckler, KDWP, unpublished data). These densities were the lowest since July-August 2004, the first year of veliger sampling, when mean lake-wide veliger density was 0.83/L. Although veliger counts may not be correlated with the number of zebra mussels that recruit to adults, invaded systems without visible adult populations of zebra mussels have been found to have veliger concentrations of less than 0.01 veligers/L (Johnson 1995; Nalepa et al. 1995). The zebra mussel population fluctuations recorded for El Dorado Reservoir were similar to population trends observed in other invaded systems. Zebra mussel population numbers in other systems, including Saginaw Bay in Lake Huron, have exhibited patterns of rapid population growth followed by a strong decline in successive years (Nalepa et al. 1995). Future monitoring will determine if the peak and subsequent drop in zebra mussel abundance in El Dorado Reservoir is part of a cyclical pattern of abundance as observed in the Hudson River (Strayer and Malcom 2006).

Zebra mussels may have affected certain macroinvertebrate taxa despite the decline in zebra mussel population density during 2008-2009. In July of the post-invasion period, amphipod abundance increased in El Dorado Reservoir, possibly contributing to a decline in Simpson’s diversity. In addition, amphipod and oligochaete abundance increased in August of the post-invasion period in El Dorado Reservoir, while chironomid abundance in El Dorado Reservoir remained consistent compared to a decrease in Melvern Reservoir, and likely contributed to a decrease in taxonomic evenness in El Dorado Reservoir. Although there was no change in taxonomic richness in either month, the effects on Simpson's diversity and taxonomic evenness are likely due to higher abundances of amphipods, oligochaetes, and chironomids in El Dorado Reservoir than in Melvern Reservoir following zebra mussel invasion. Although amphipods, chironomids, and oligochaetes may benefit from zebra mussel invasion, a number of other invertebrate taxa have shown no response to zebra mussel invasion (Stewart et al. 1998; Beekey et al. 2004). The effect on amphipods, chironomids, and oligochaetes is possibly related to the increased habitat surface area, habitat heterogeneity, and available benthic organic matter provided by zebra mussel colonization (Stewart et al. 1998). The shells of dead zebra mussels often remain attached to substrate and continue to be used by macroinvertebrate fauna (Stewart et al. 1998). Interstitial spaces between zebra mussel shells may provide amphipods, chironomids, and oligochaetes with shelter from predators and wave action, and may trap organic material and provide additional food resources for chironomids and oligochaetes (Ricciardi et al. 1997; Stewart et al. 1998; Gonzalez and Downing 1999). In addition, predaceous macroinvertebrates, including some chironomid taxa, may be attracted to zebra mussel beds by the abundance of macroinvertebrate prey (Stewart et al. 1998). Horvath et al. (1999) found that benthic organic matter may not accumulate at low zebra mussel densities, indicating that increases in habitat area and heterogeneity from living and dead mussels may contribute more directly to increased macroinvertebrate abundance than the increase in benthic organic matter. Due to the low numbers of live zebra mussels present in El Dorado Reservoir during the study period (live zebra mussels were observed at less than 10% of sampling sites in El Dorado Reservoir, and observed live zebra mussel densities did not exceed 100/m^2) in comparison to abundances in 2005-2006 (up to 65,000 zebra mussels/m^2, J. Goeckler, Kansas Department of Wildlife and Parks, personal communication), the increase in mean total macroinvertebrates, amphipods, oligochaetes, and the maintenance of a consistent level of chironomids in comparison to Melvern Reservoir may be the result of habitat enhancement provided by mussel shells that remain from previous population peaks. The cause for an increase in macroinvertebrate taxa in August but not July may be related to predator avoidance. Gonzalez and Downing (1999) previously found that amphipods in Lake Erie preferred habitat with zebra mussels in August, when predation risk from fishes including bluegill increased in comparison to June and July. Thus, zebra mussel invasion in El Dorado Reservoir may have benefitted some macroinvertebrates by providing increased habitat surface area and heterogeneity that is suitable for amphipods, chironomids, and oligochaetes.

Our results indicated a decline in littoral fish abundance in El Dorado Reservoir during the summer months following zebra mussel establishment. The decline in August may be the result of the reduced abundance of *Lepomis* spp. and red shiner, which composed over 53% of the total catch. *Lepomis* spp. and red shiners feed extensively on macroinvertebrates during the summer months, although bluegill may also consume large amounts of zooplankton depending on their size class (Greger and Deacon 1988; Olson and Nickol 1996; Gonzalez and Downing 1999; Harris et al. 1999). The increased habitat heterogeneity provided by zebra mussel shell beds may increase the ability of amphipods, chironomids, and oligochaetes to seek shelter in zebra mussel beds, reducing prey availability for *Lepomis* spp. and red shiners. It may also be possible that bluegill were switching to pelagic habitat upon encountering reduced benthic prey, thus reducing their abundance in the littoral zone (Werner and Hall 1979; Werner and Hall 1988; Harris et al. 1999).

Largemouth bass growth had a greater increase in El Dorado Reservoir than Melvern Reservoir during the summer months following zebra mussel invasion, but the differences in these growth rates (about 5%) may not be biologically meaningful. The change in growth rate and lack of decline in zooplankton abundance does not support our hypothesis that zebra mussel presence would reduce zooplankton abundance, which in turn would decrease largemouth bass growth rates in El Dorado Reservoir. Total zooplankton abundance remained relatively constant between reservoirs throughout the study. However, this small difference in growth between the two reservoirs may be due to the increased macroinvertebrate abundance in El Dorado Reservoir. Strakosh (2006) found that amphipods were present in 0-6.4% of age-0 largemouth bass diets, and chironomids were present in 0-13.8% of age-0 largemouth bass diets in El Dorado and Melvern reservoirs prior to zebra mussel invasion. In addition, largemouth bass growth may also be affected by a variety of abiotic factors, including water temperature, turbidity, and water levels (Parkos and Wahl 2002). Further diet and foraging analysis and inclusion of abiotic variables may be needed to better determine zebra mussel effects on age-0 largemouth bass growth.

Additional monitoring of zebra mussel population dynamics in El Dorado Reservoir, including continued sampling of zooplankton, macroinvertebrates, and fish, would be beneficial to determine the long-term effects of zebra mussel invasion in Great

Plains reservoirs. Sampling of biota during times of high zebra mussel abundance may reveal whether zebra mussels were able to reduce zooplankton abundance in turbid, warm-water reservoirs which frequently exceed the preferred thermal range of zebra mussels (17-23° C; Ludyanskiy et al. 1993) in the summer, and whether this impacts zooplanktivorous fishes. In addition, continued monitoring of zebra mussel beds, both with live and dead mussels, would provide additional insight into how zebra mussel beds affect macroinvertebrate abundance in reservoir systems, including whether the observed increase in some macroinvertebrate taxa was only a seasonal phenomenon, or whether this becomes a more consistent trend over time.

In conclusion, our results indicate that the low-density zebra mussel population observed in El Dorado Reservoir, Kansas, in 2008-2009 has had minimal impact on zooplankton abundance and community structure. However, remnant zebra mussel beds from abundance peaks in 2005-2006 appear to benefit some macroinvertebrate taxa, but may disadvantage some invertivorous fishes including *Lepomis* spp. and red shiners. It is important to note that the effects hypothesized for zooplankton in El Dorado Reservoir depended upon a large living population of zebra mussels in El Dorado Reservoir, which was not observed during the post-invasion fieldwork, and was not reflected in the reported veliger densities. In contrast, zebra mussel shell beds and shell litter remained at most sampling sites during the post-invasion sampling period, which may be enough to affect the macroinvertebrate community of El Dorado Reservoir. These effects on macroinvertebrates may in turn continue to affect the fish community of El Dorado Reservoir even after a zebra mussel population decline. However, our results are based on only two years of pre- and two years of post-zebra mussel invasion data. Other research has suggested that considerable short-term variability may exist in zebra mussel population dynamics and ecological responses to zebra mussel invasion, and longer-term studies may provide different results (Nalepa et al. 2003; Barbiero et al. 2006; Caraco et al. 2006; Strayer and Malcom 2006; Fernald et al. 2007). In addition, Mayer et al. (2000) and Strayer et al. (2004) recommended use of long-term datasets to better understand effects of zebra mussel invasion, and Mayer et al. (2000) suggested that datasets with less than five years of post-invasion fish data may be insufficient because of reduced statistical power. Nonetheless, our research provides some evidence of the effects of zebra mussels on littoral zone aquatic biota in reservoirs, and could provide the basis for future studies and hypotheses on the long-term effects of zebra mussels in these systems.

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Table 1.1 Percent total catch of all fish species caught in littoral zone electrofishing sampling at El Dorado and Melvern reservoirs for two years pre-zebra mussel invasion (2001-2002) and two years post-zebra mussel invasion (2008-2009).

Scientific Name	Common Name	Percent Total Catch (N = 6,707)
Aplodinotus grunniens	Freshwater drum	0.25
Campostoma anomalum	Central stoneroller	0.43
Cyprinella lutrensis	Red shiner	13.28
Cyprinus carpio	Common carp	0.06
Dorosoma cepedianum	Gizzard shad	3.53
Etheostoma nigrum	Johnny darter	0.16
Etheostoma spectabile	Orangethroat darter	2.27
Fundulus notatus	Blackstripe topminnow	1.36
Gambusia affinis	Western mosquitofish	5.65
Ictalurus punctatus	Channel catfish	1.61
Ictiobus spp.	Age-0 buffalo (bigmouth/smallmouth)	0.03
Lepisosteus osseus	Longnose gar	0.21
Lepomis cyanellus	Green sunfish	6.23
Lepomis humilis	Orangespotted sunfish	3.13
Lepomis macrochirus	Bluegill	2.59
Lepomis megalotis	Longear sunfish	0.24
Lepomis spp.	Age-0 and hybrid sunfish	27.98
Micropterus dolomieu	Smallmouth bass	0.03
Micropterus punctulatus	Spotted bass	0.03
Micropterus salmoides	Largemouth bass	2.30
Morone chrysops	White bass	0.12
Notropis stramineus	Sand shiner	0.75
Noturus exilis	Slender madtom	0.16
Percina caprodes	Logperch	3.82
Percina phoxocephala	Slenderhead darter	3.09
Phenacobius mirabilis	Suckermouth minnow	0.78
Pimephales notatus	Bluntnose minnow	14.79
Pimephales promelas	Fathead minnow	0.12
Pimephales vigilax	Bullhead minnow	1.04
Pomoxis annularis	White crappie	0.16
Pylodictis olivaris	Flathead catfish	0.12

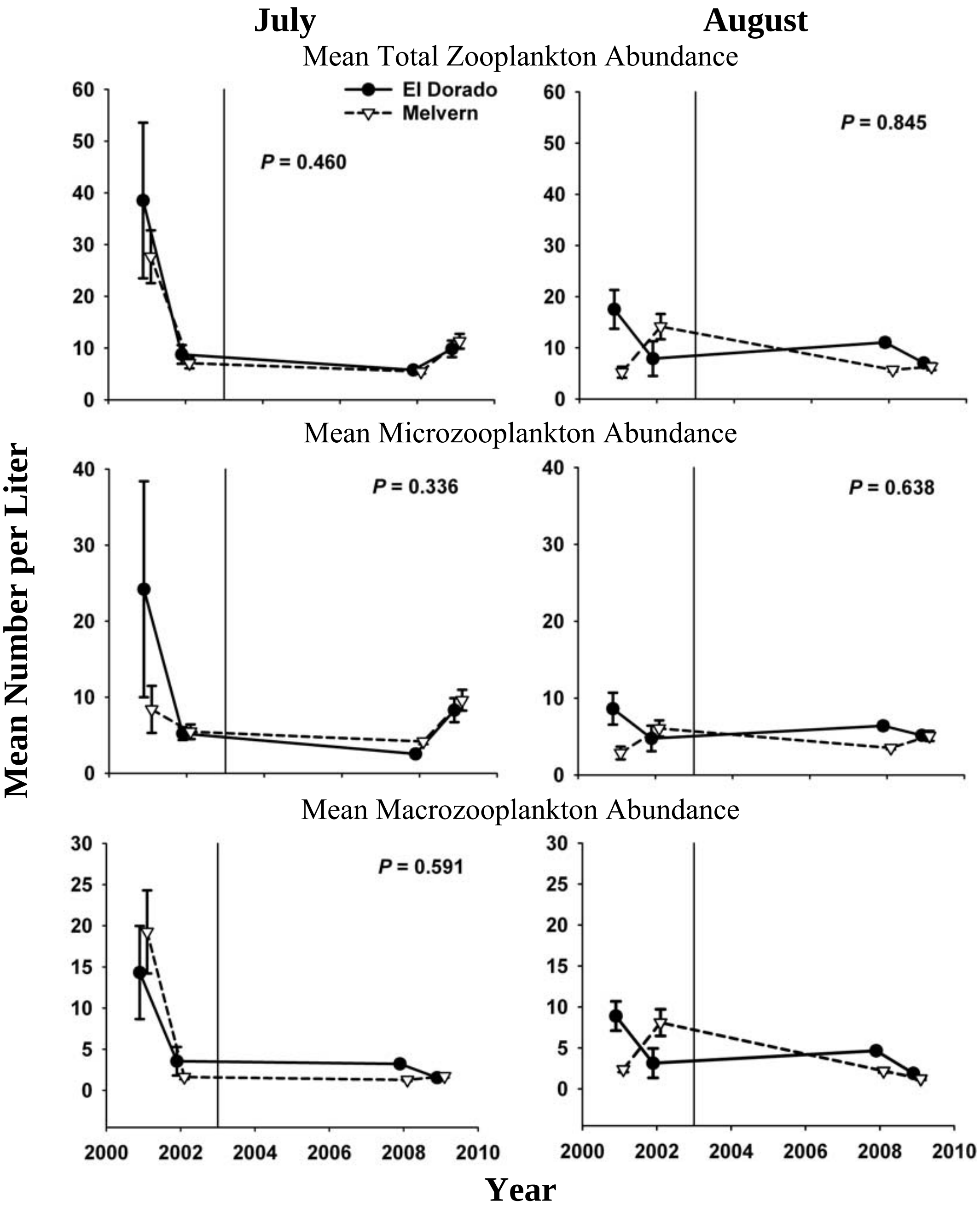


Figure 1.1 Mean total zooplankton abundance, microzooplankton abundance, and macrozooplankton abundance for July and August in El Dorado and Melvern reservoirs. Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. *P*-values test if trends in zooplankton abundance were consistent between reservoirs in the pre- and post-zebra mussel invasion periods.

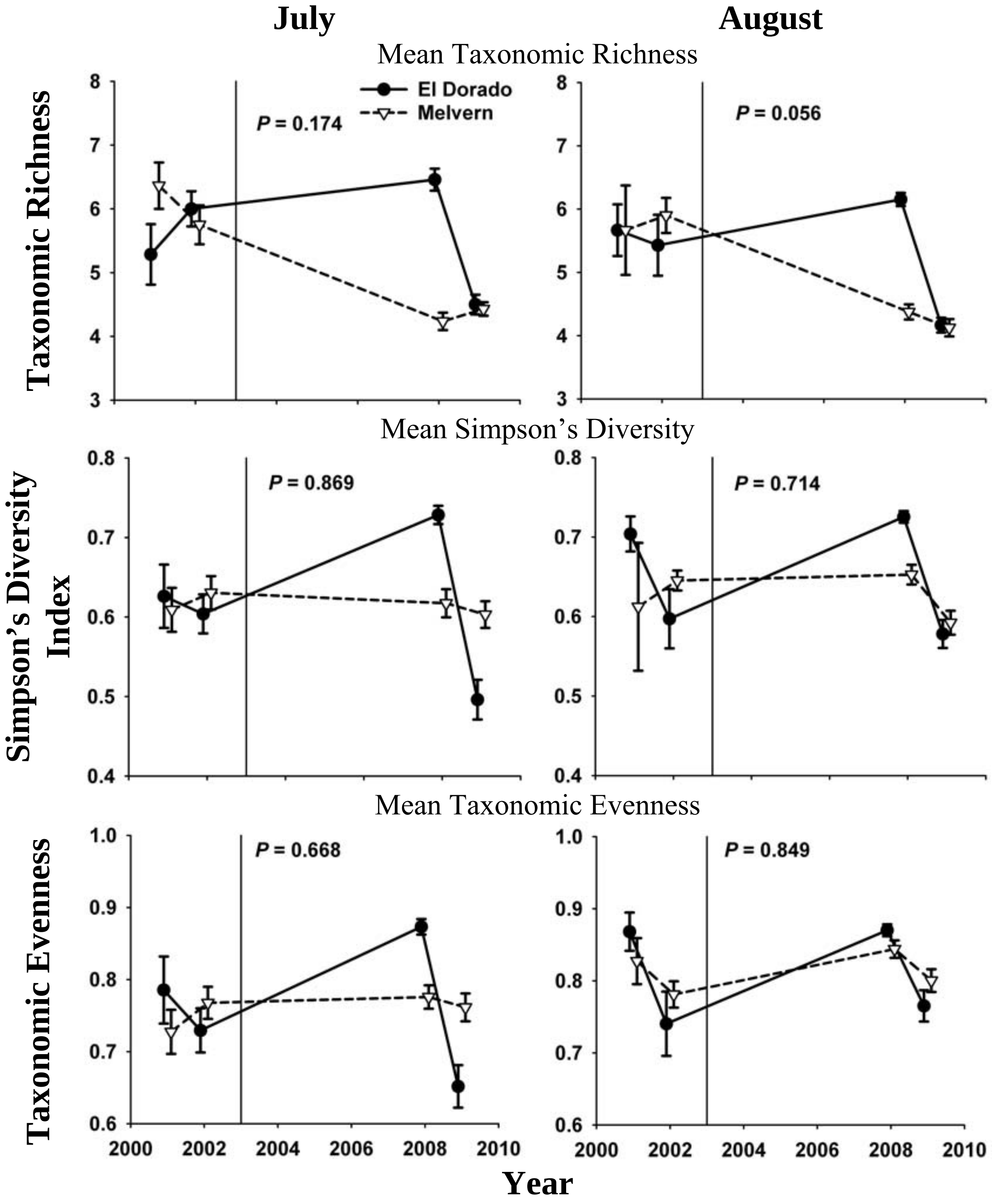
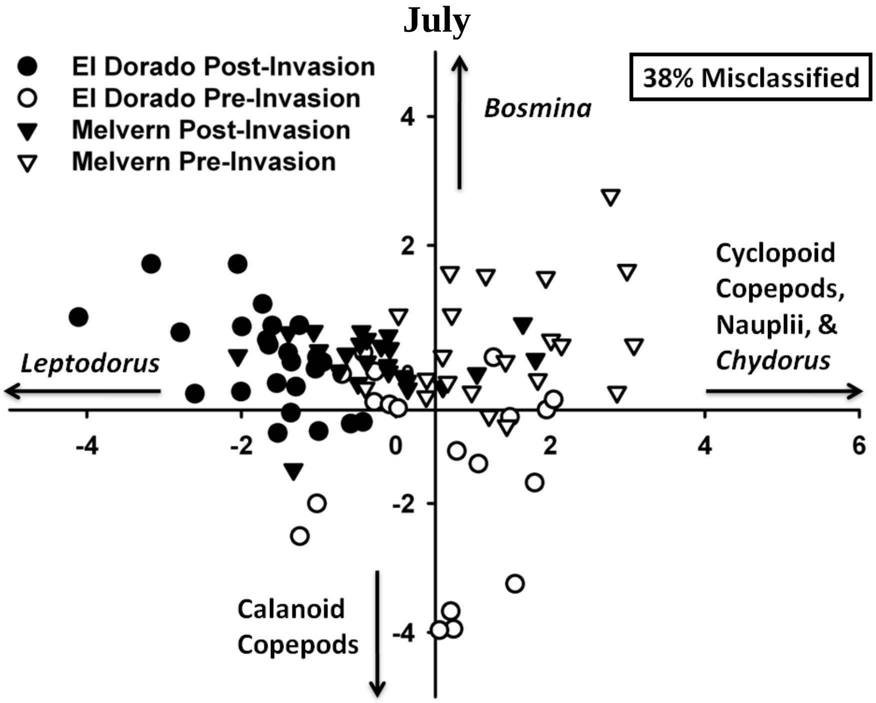


Figure 1.2 Mean taxonomic richness, Simpson's diversity index, and taxonomic evenness for zooplankton communities of El Dorado and Melvern reservoirs in July and August. Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. *P*-values test if trends in zooplankton community indices were consistent between reservoirs in the pre- and post-zebra mussel invasion periods.



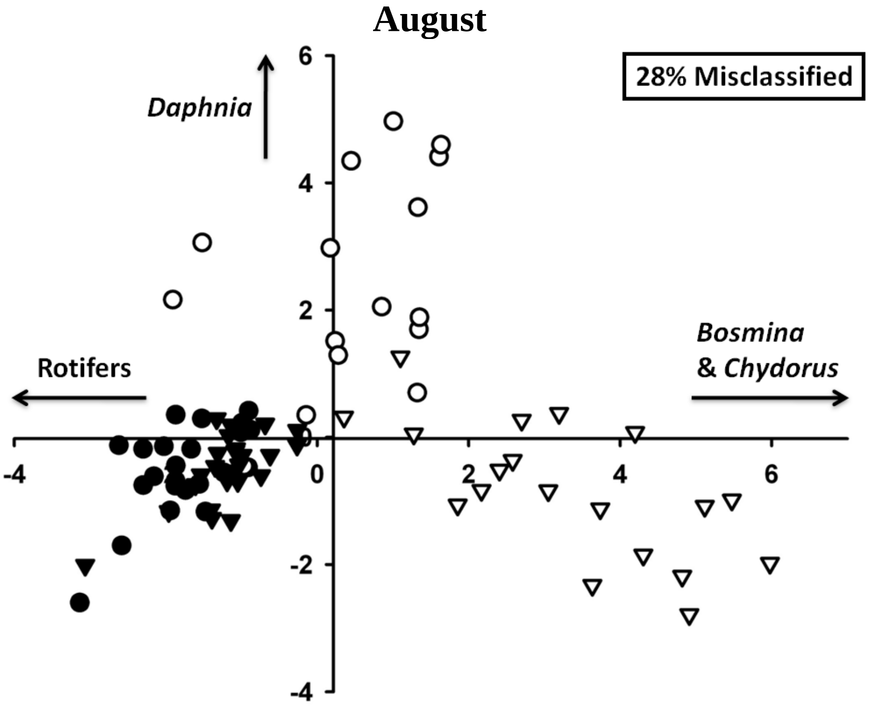


Figure 1.3 Discriminant analyses of zooplankton taxa abundance in El Dorado and Melvern reservoirs in July (top) and August (bottom) prior to zebra mussel invasion (2001-2002) and after zebra mussel invasion (2008-2009).

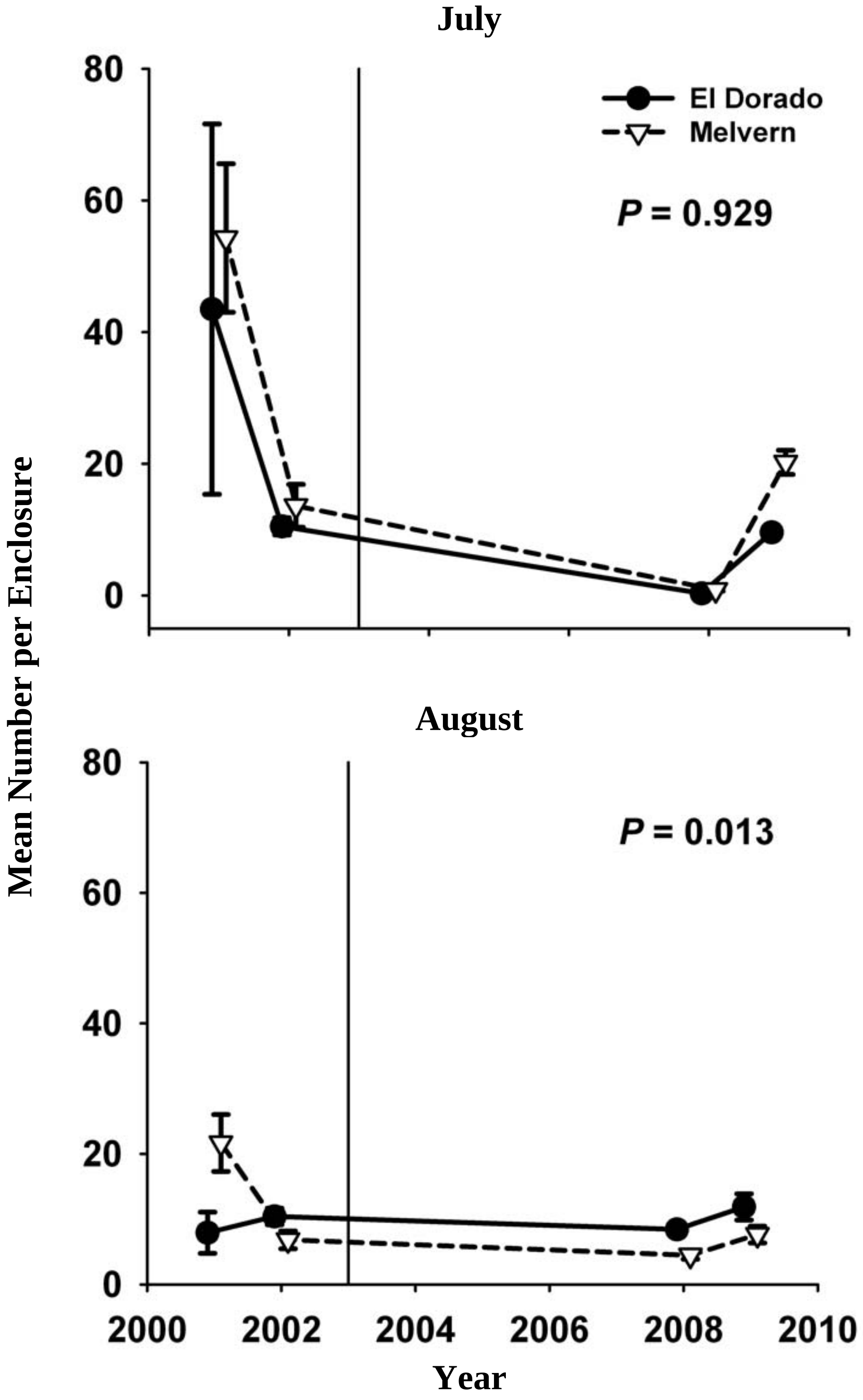


Figure 1.4 Mean total benthic macroinvertebrate abundance in the littoral zone of El Dorado and Melvern reservoirs in July and August of 2001-2002 and 2008-2009. Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. *P*-values test if trends in mean total benthic macroinvertebrate abundance were consistent between reservoirs in the pre- and post-zebra mussel invasion periods.

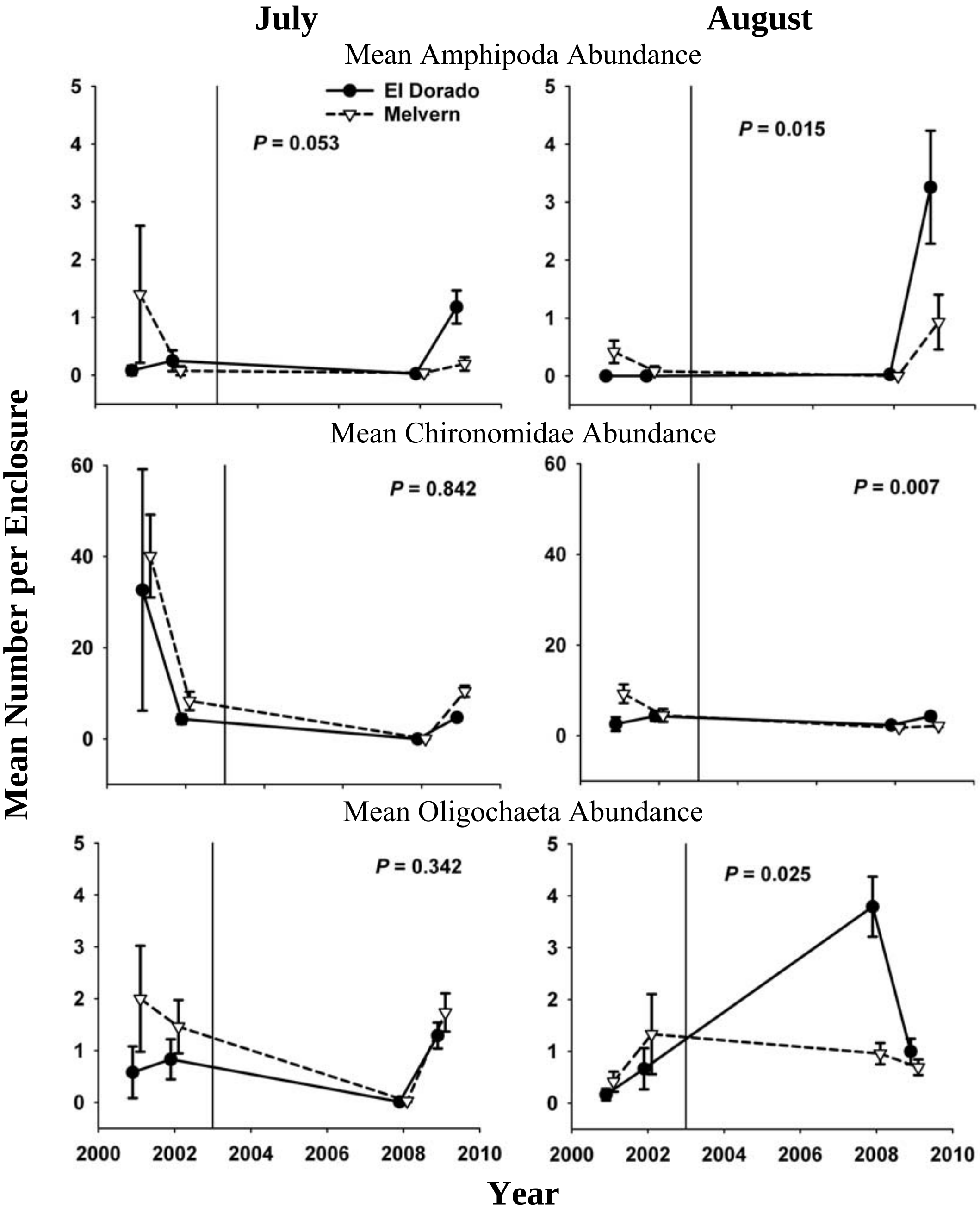


Figure 1.5 Mean Amphipoda, Chironomidae, and Oligochaeta abundance for July and August in El Dorado and Melvern reservoirs. Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. *P*-values test if trends in macroinvertebrate abundance were consistent between reservoirs in the pre- and post-zebra mussel invasion periods.

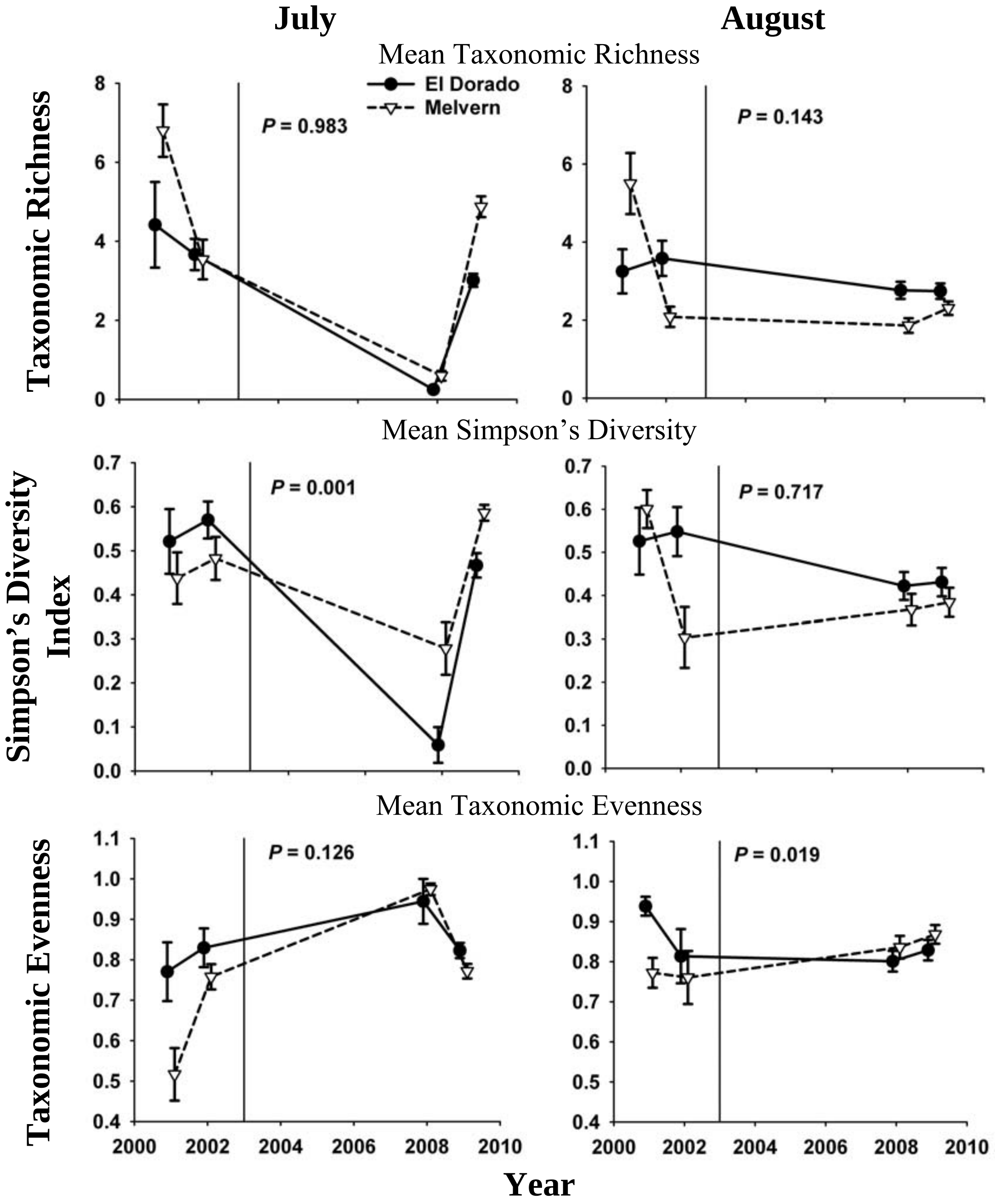


Figure 1.6 Mean taxonomic richness, Simpson's diversity index, and taxonomic evenness for macroinvertebrate communities of El Dorado and Melvern reservoirs in July and August. Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. *P*-values test if trends in macroinvertebrate community indices were consistent between reservoirs in the pre- and post-zebra mussel invasion periods.

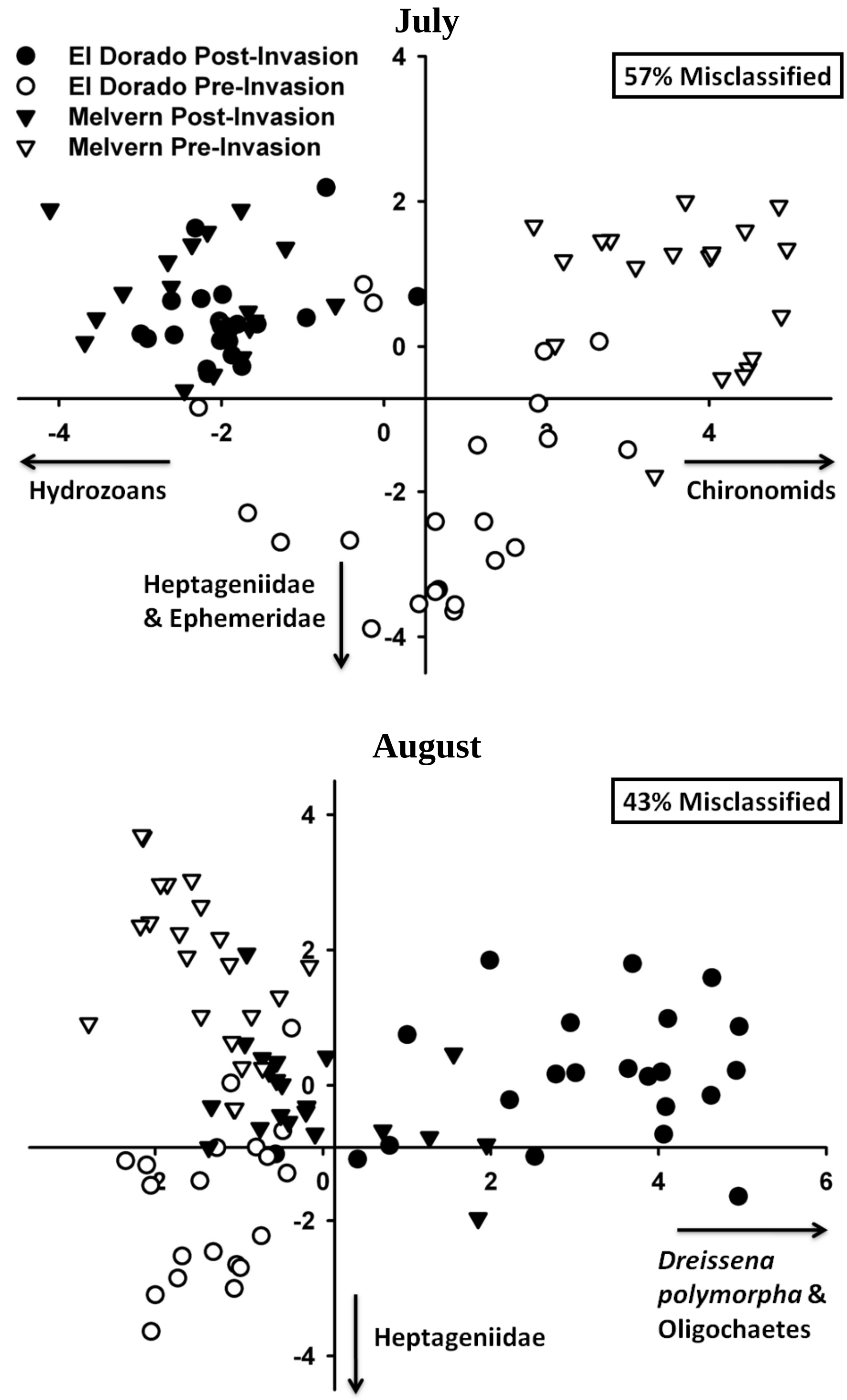


Figure 1.7 Discriminant analyses of benthic macroinvertebrate taxa abundance in El Dorado and Melvern reservoirs in July (top) and August (bottom) prior to zebra mussel invasion (2001-2002) and after zebra mussel invasion (2008-2009).

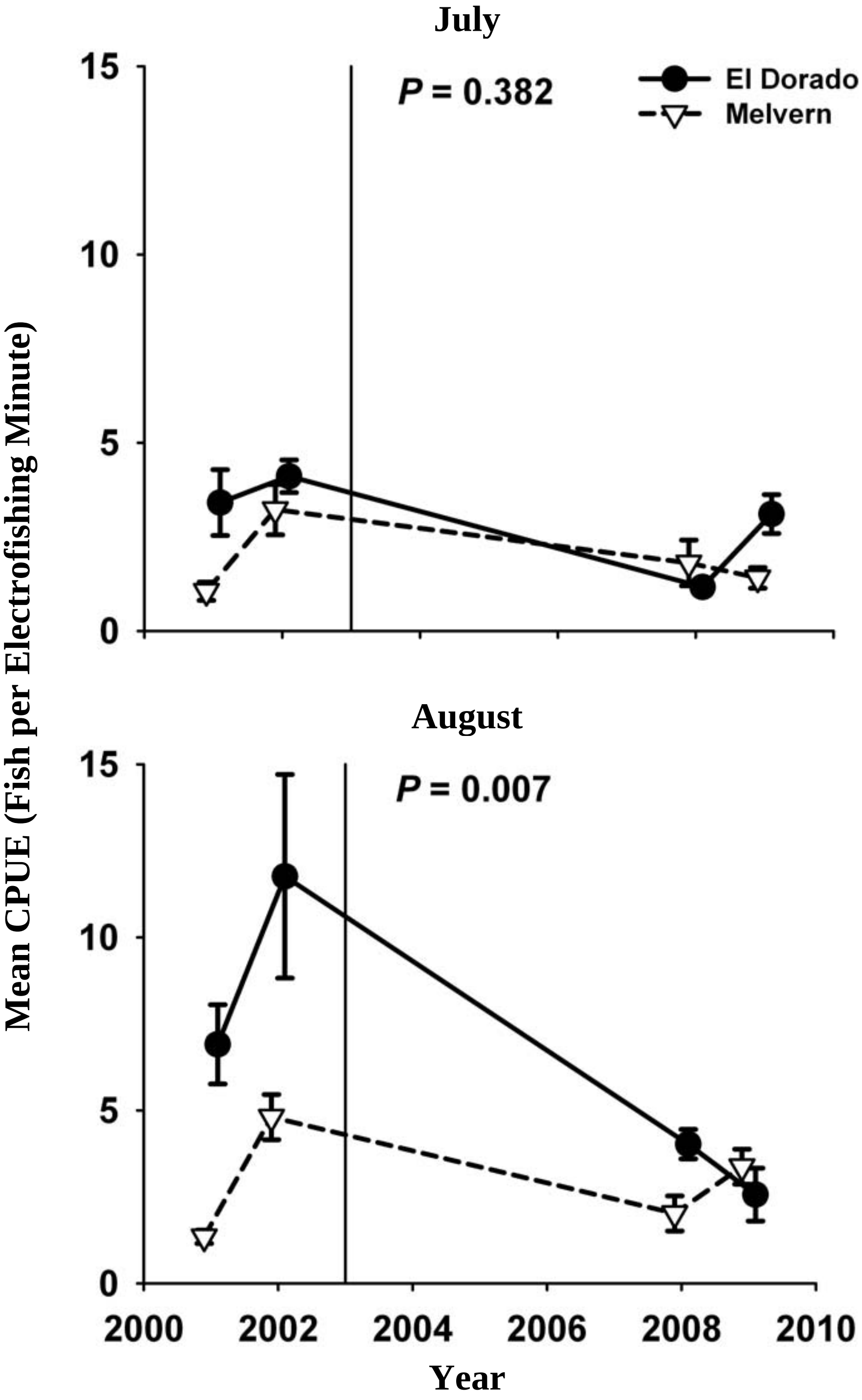


Figure 1.8 Mean total catch per unit effort (fish per electrofishing minute) of juvenile and small-bodied fishes in the littoral zone of El Dorado and Melvern reservoirs in July and August of 2001, 2002, 2008, and 2009. Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. *P*-value tests if trends in mean CPUE were consistent between reservoirs in the pre- and post-zebra mussel invasion periods.

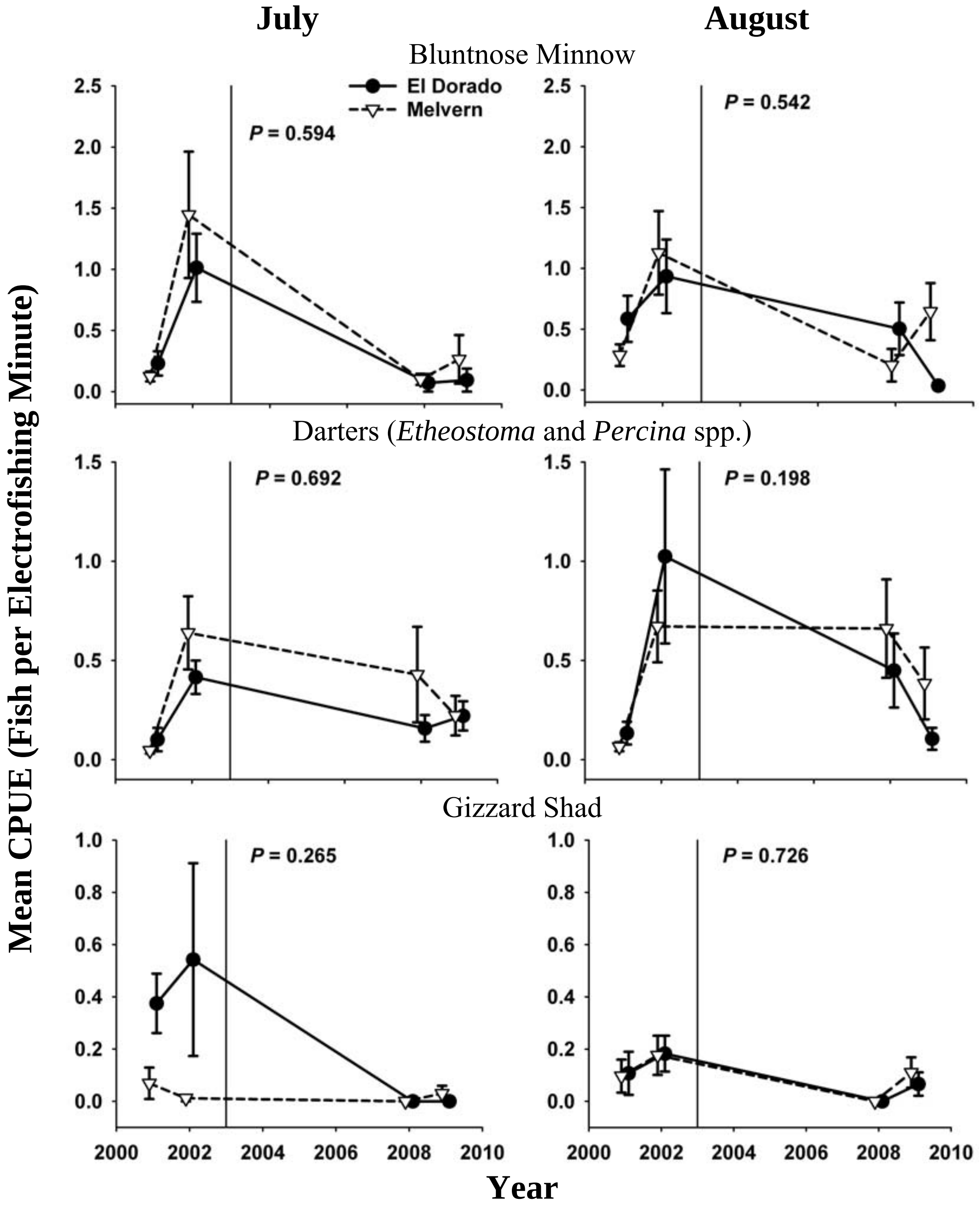


Figure 1.9 Mean catch per unit effort of bluntnose minnow, darters (Johnny darter, logperch, orangethroat darter, and slenderhead darter), and gizzard shad in the littoral zone of El Dorado and Melvern reservoirs in July and August of 2001, 2002, 2008, and 2009. Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. *P*-value tests if trends in mean CPUE were consistent between reservoirs in the pre- and post-zebra mussel invasion periods.

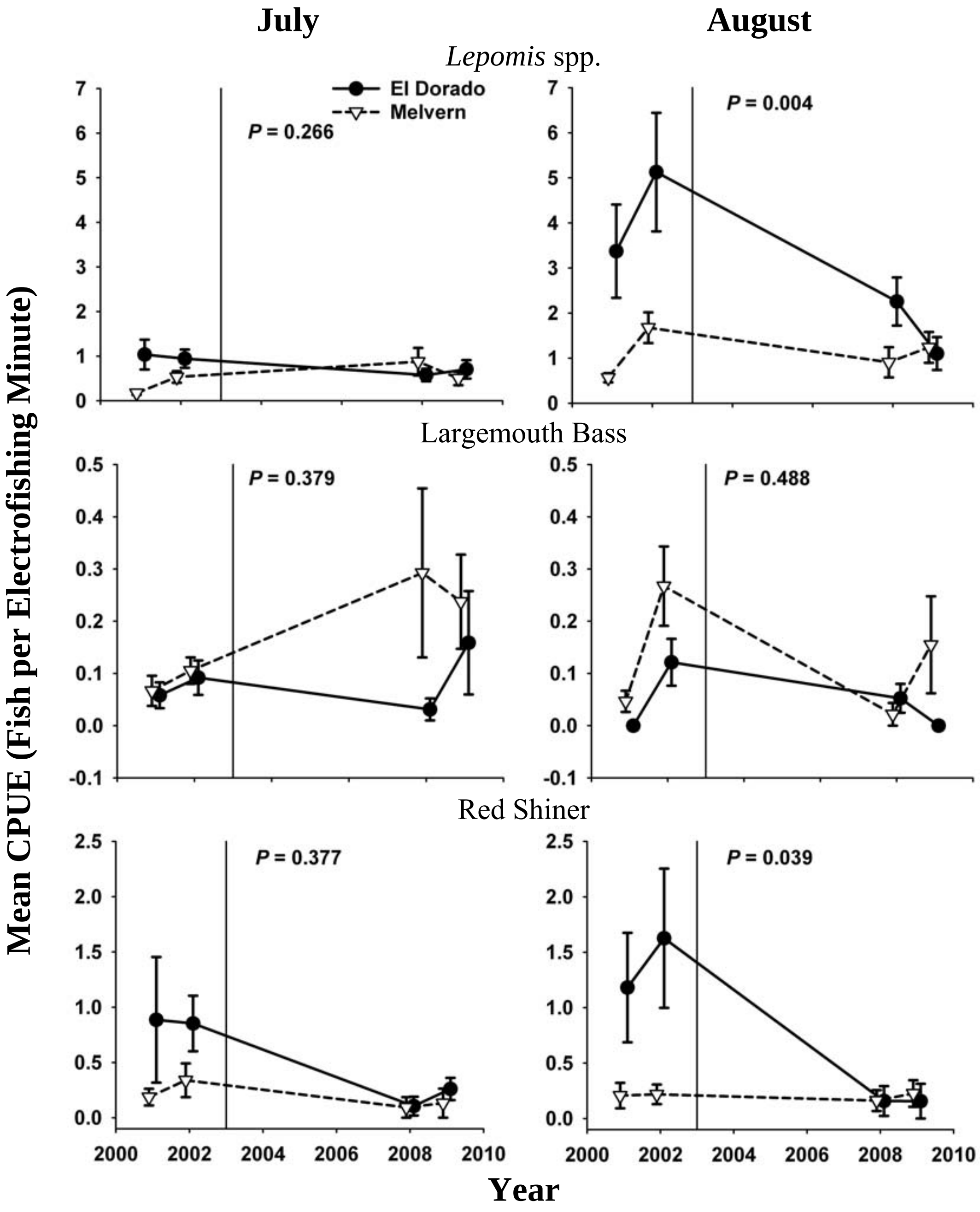


Figure 1.10 Mean catch per unit effort (fish per electrofishing minute) of *Lepomis* spp. (bluegill, green sunfish, longear sunfish, hybrid sunfish, and unidentifiable age-0 *Lepomis* spp.), largemouth bass, and red shiners in the littoral zone of El Dorado and Melvern reservoirs in July and August of 2001, 2002, 2008, and 2009. Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. *P*-value tests if trends in mean CPUE were consistent between reservoirs in the pre- and post-zebra mussel invasion periods.

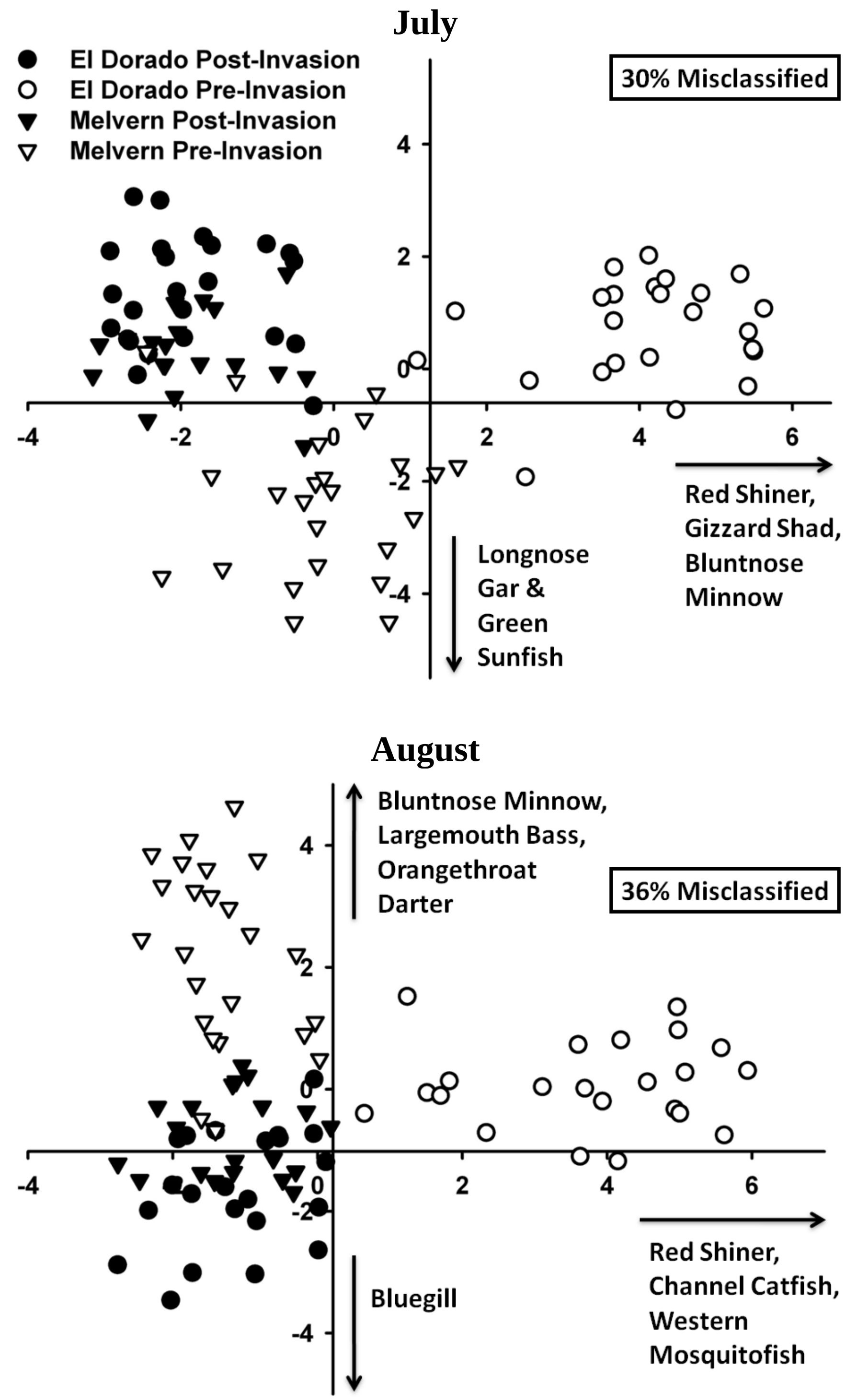


Figure 1.11 Discriminant analyses of fish taxa abundance in El Dorado and Melvern reservoirs in July (top) and August (bottom) prior to zebra mussel invasion (2001-2002) and after zebra mussel invasion (2008-2009).

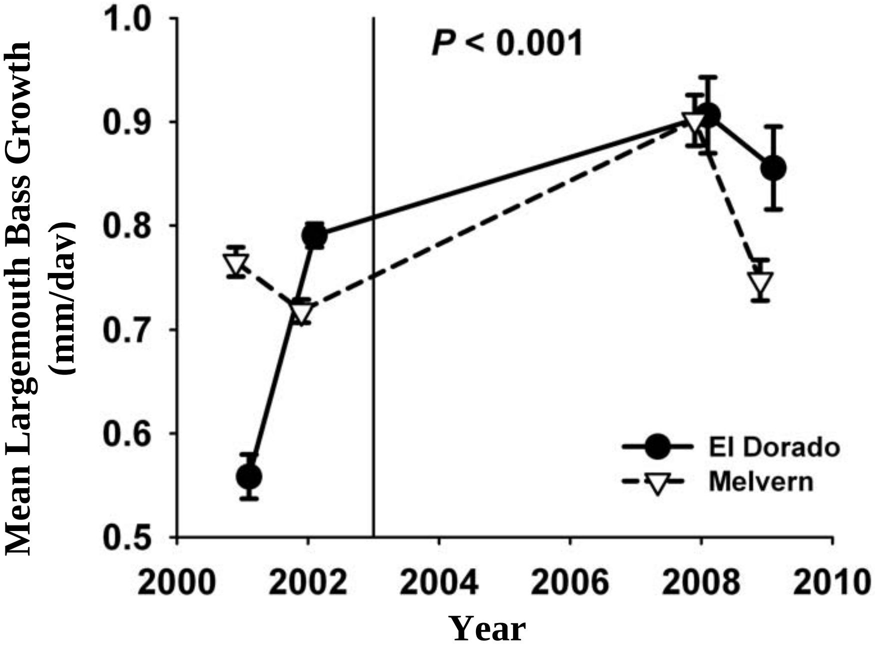


Figure 1.12 Mean growth (mm/day) of age-0 largemouth bass in El Dorado and Melvern reservoirs in July and August (both months combined) of 2001, 2002, 2008, and 2009. Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. *P*-value tests if trends in growth were consistent between reservoirs in the pre- and post-zebra mussel invasion periods.

CHAPTER 2 - Effects of zebra mussel invasion on adult fishes of El Dorado Reservoir

Introduction

One of the primary concerns in ecology is the effect of biological invasions. If non-native species become successfully established, they may continue to broaden their range and affect native species and habitats. Some of these impacts can be economically and environmentally costly (Lockwood et al. 2007). However, some of these invasions, including zebra mussel (*Dreissena polymorpha*) invasion in North America, have impacts that may not yet be fully realized.

The zebra mussel is a bivalve native to the Caspian, Black, and Azov Seas of Eurasia, but was introduced to the North American Great Lakes in the mid-1980s via bilge water, and has been classified as an invasive species (Karatayev et al. 1997; Lockwood et al. 2007). Zebra mussels have spread throughout much of the Eastern US and the Great Plains (Lockwood et al. 2007). Although research has been conducted on the impacts of zebra mussels on aquatic food webs in the Great Lakes region (cool- to cold-water natural lakes), little attention has been given to possible effects of zebra mussels in the turbid, warm-water reservoirs of the Great Plains.

Zebra mussels may exert a bottom-up influence on aquatic food webs and ultimately impact fish. Phytoplankton is the primary food source for zebra mussels and grazing zooplankton, and reduction of phytoplankton abundance by zebra mussels may create food limitations for zooplankton (Strayer et al. 1999; Trometer and Busch 1999; Raikow 2004). In addition, zebra mussel consumption of microzooplankton (rotifers, nauplii) may directly reduce microzooplankton abundance, resulting in food limitations for zooplanktivorous fish, which may lead to decreased growth and/or abundance of planktivorous fishes (MacIsaac 1996; Strayer et al. 1999). The larval stages of fish (including piscivores) are frequently zooplanktivorous, and a lack of food in the larval stage could lead to stunted growth, decreasing the probability of overwinter survival (Garvey and Stein 1998; Raikow 2004).

Zooplanktivorous fish often form the basis of piscivorous fish diets. Age-0 bluegill (*Lepomis macrochirus*) and gizzard shad (*Dorosoma cepedianum*) are key components of largemouth bass (*Micropterus salmoides*) and walleye (*Sander vitreus*) diets in lakes and reservoirs (Olson 1996; Garvey and Stein 1998; Kolar et al. 2003; Quist et al. 2004). Age-0 gizzard shad are the primary prey for age 1+ white bass (*Morone chrysops*) in many Great Plains reservoirs, and age-0 gizzard shad abundance during the summer and fall is a key determinant of white bass condition throughout the year (Guy et al. 2002). Growth of piscivorous fishes is closely linked to the abundance of their preferred zooplanktivorous prey species (Kolar et al. 2003; Garvey and Stein 1998). Therefore, decline in abundance of zooplanktivorous fish species associated with zebra mussel presence may result in negative effects for piscivorous predators.

Objectives

Our objective was to determine whether the abundance and condition of adult fishes declined with zebra mussel presence in a warm-water reservoir. We hypothesized that zebra mussel invasion would lead to reduced abundance and condition of adult fishes via two pathways: 1) a reduction in zooplankton due to zebra mussels would reduce growth and survival of age-0 reservoir fishes, leading to reduced abundance and condition of these fishes beyond age-0; 2) reduced growth and survival of age-0 fishes would reduce the amount of forage available to piscivorous adult fishes, leading to a decline in abundance and condition of these adult fishes. We focused on bluegill, gizzard shad, largemouth bass, walleye, white bass, and white crappie (*Pomoxis annularis*) for this study because they are common reservoir fishes in the Great Plains region.

We used a before-after control-impact (BACI) study design to determine if mean relative abundance and condition of the six fish species differed between one impacted reservoir (El Dorado Reservoir) and three control reservoirs (Clinton, Marion, and Milford reservoirs) before and after zebra mussel invasion. Three control systems with similar hydrologic and habitat characteristics were used to provide replication (Underwood 1994). In the BACI design, overall effect of impact is determined by the mean difference in a particular metric (abundance, condition) between the control and impacted systems before and after the impact occurred (Smith 2002).

Study Sites

Four large (>2800 ha) federal reservoirs in Eastern Kansas—Clinton, El Dorado, Marion, and Milford—were chosen as the study sites based on input from Kansas Department of Wildlife and Parks (KDWP) biologists. These reservoirs had relatively similar watersheds and hydrologic characteristics (Table 2.1). Mean summer water temperature in Eastern Kansas reservoirs generally ranged between 28-30° C, mean dissolved oxygen ranged between 6-7 mg/L, and mean turbidity ranged between 21-33 NTU (Quist et al. 2004; Strakosh et al. 2009). Largemouth bass and walleye are regularly stocked in all study reservoirs. Zebra mussels were confirmed in El Dorado Reservoir in 2003. Sampling was conducted for ten years pre-zebra mussel invasion (1993-2002) and five years post-invasion (2004-2008). Mean summer veliger densities

(June-August) in El Dorado Reservoir ranged from 4.24/L (2004) to 116.78/L (2006) throughout the post-invasion period, with densities exceeding 100 veligers/L only in 2006 (J. Goeckler, KDWP, unpublished data). Clinton and Milford Reservoirs remained free of zebra mussels throughout the entire study period. Zebra mussel presence was confirmed in the final year of the study (summer 2008) in Marion Reservoir.

Methods

Field Methods

We analyzed data collected by KDWP biologists as part of a long-term standardized reservoir sampling protocol for ten years pre-zebra mussel invasion (1993-2002) and five years post-invasion (2004-2008). Gizzard shad, walleye, and white bass were sampled via annual fall gillnetting. Individual monofilament gill nets (30.5 m x 2.4 m) of each of three bar mesh sizes (2.5, 3.8, 6.4 cm) were set together as complements. Five net complements per year (15 individual nets) was the minimum sampling requirement for Clinton, El Dorado, and Marion reservoirs; minimum effort for Milford Reservoir was six net complements (18 individual nets) per year. Each individual gill net represented one unit of effort. Bluegill and white crappie were sampled with a minimum of sixteen 1.3-cm or 2.5-cm trap nets (1.2 m x 1.5 m) set over night during the fall. Each individual trap net was considered one unit of effort. Both net types (gill net and trap net) were set at fixed sites before sunset and retrieved after sunrise the following day. Largemouth bass were sampled using boat electrofishing during spring (220-250 V pulsed DC, 5-10 A) in ten minute increments at a minimum of ten locations per reservoir. Length and weight data was collected in the field for all captured fish (Marteney and Mosher 2004). Catch per unit effort (CPUE; fish per trap net/gill net or electrofishing hour) and relative weight (W_r) were calculated for stock-to-quality length fish and used as indices of abundance and condition, respectively. Stock-to-quality length fish are generally age 1-4 in the Great Plains ecoregion (Brouder et al. 2009). Length classes and relative weights for all species were determined according to Anderson and Neumann (1996). Weight data from 2006 was omitted due to mechanical problems with the scales used at El Dorado Reservoir (C. Johnson, Kansas Department of Wildlife and Parks, personal communication).

Experimental Design and Statistical Analysis

A 2-way analysis of covariance (ANCOVA) with interactions was used with linear orthogonal contrasts to determine if mean CPUE for each species differed by time period (before/after) or impact (control/zebra mussel). Because water level fluctuation can influence reservoir fishes (Martin et al. 1981; Parkos and Wahl 2002), we included mean seasonal water level fluctuation (difference from conservation pool elevation) for spring (March-May), summer (June-August), fall (September-November), and winter (December-February) as covariates. A 2-way ANCOVA (mean seasonal water level fluctuation as covariate) with interactions and linear orthogonal contrasts was also used to determine whether mean W_r for each species differed by time period (before/after) or impact (control/zebra mussel). Largemouth bass abundance and condition data was only analyzed from El Dorado and Clinton reservoirs due to no largemouth bass data for at least 40% of years in Marion and Milford reservoirs. All analyses were completed with SAS 9.1.3 (SAS Institute Inc., Cary, North Carolina). A significant contrast ($P < 0.05$) indicated divergent trends in abundance or condition (i.e. trends in abundance or condition were not consistent among the impacted and control reservoirs between the pre- and post-invasion time periods).

Results

Abundance

No stock-to-quality length bluegill were caught in El Dorado Reservoir in 1995-1996 and 1998, and in Marion Reservoir in 1999, 2002, and 2005; sampling was not conducted at Marion Reservoir in 1994 and 1997. Mean bluegill CPUE ranged from 0.06 (SE = 0.06; Milford 1995) to 67.81 (SE = 52.43; Milford 2000), but trends in abundance did not diverge between El Dorado Reservoir and the control reservoirs across time periods (*P*s > 0.528; Figure 2.1; Tables 2.2, 2.4, 2.5; See Appendix B.1). No gizzard shad were caught in El Dorado Reservoir in 1993, 1996-1998, and 2001, in Marion Reservoir in 1993, and in Milford Reservoir in 1993-1996 and 2005. Mean gizzard shad CPUE ranged from 0.06 (SE = 0.06; Marion 2008) to 39.38 (SE = 26.87; Marion 1996), and trends in abundance remained consistent among reservoirs across time (*P*s > 0.158; Figure 2.1; Tables 2.2, 2.4, 2.5). No largemouth bass were caught in El Dorado Reservoir in 2008; sampling was not conducted at El Dorado Reservoir in 1995 or at Clinton Reservoir in 1993, 1995, and 2007-2008. Mean largemouth bass CPUE ranged from 0.69 (SE = 0.38; Clinton 2004) to 6.65 (SE = 1.33; El Dorado 2004), and was consistent between reservoirs across time (*P*s > 0.154; Figure 2.1; Tables 2.2, 2.4, 2.5). Mean walleye CPUE ranged from 0.08 (SE = 0.08; Clinton 2007) to 5.29 (SE = 1.55; Marion 1993), and was similar among reservoirs across time (*P*s > 0.258; Figure 2.1; Tables 2.2, 2.4, 2.5). No white bass were caught in El Dorado Reservoir in 1996. Mean white bass abundance (fish per gill net) ranged from 0.13 (SE = 0.13; El Dorado 2008) to

45.42 (SE = 18.29; Marion 2001), and was similar among all reservoirs across time (*P*s > 0.415; Figure 2.1; Tables 2.2, 2.4, 2.5). No white crappie were caught in El Dorado Reservoir in 1997; sampling was not conducted at Marion Reservoir in 1994 and 1997. Mean white crappie abundance (fish per trap net) ranged from 0.08 (SE = 0.06; Clinton 2008) to 44.54 (SE = 5.94; Clinton 1997). However, mean white crappie CPUE in El Dorado Reservoir declined from 2.68 fish per trap net (SE = 0.41) in the pre-invasion period to 2.07 fish per trap net (SE = 0.46) in the post-invasion period (23% decline), whereas mean white crappie CPUE in the control reservoirs declined by an average of 71% from the pre-invasion to the post-invasion period (*P*s < 0.028; Figure 2.1; Tables 2.2, 2.4, 2.5). Thus, white crappie abundance declined in all systems in the post-invasion time period, but the magnitude of the decline was greater in the control reservoirs than in El Dorado Reservoir.

Condition

No bluegill length-weight data were collected in Clinton Reservoir in 1993, 1995-1997, 2000, 2004, and 2007, in El Dorado Reservoir in 1995-1996, 1998, 2004, and 2008, in Marion Reservoir in 1994, 1997, 1999, 2002, and 2005, and in Milford Reservoir in 1998 and 2002. Mean bluegill relative weight ranged from 75.01 (SE = 5.96; El Dorado 2002) to 128.44 (Milford 1995). However, mean relative weight of bluegill in El Dorado Reservoir declined from 104.09 (SE = 1.99) in the pre-invasion period to 95.63 (SE = 1.29) in the post-invasion period (8% decline), while mean relative weight increased by an average of 4% in the control systems over the same time period (*P*s < 0.002; Figure 2.2; Tables 2.3, 2.4, 2.5; See Appendix B.2). Gizzard shad relative weight data were not analyzed because stock-to-quality gizzard shad length-weight data was collected from El Dorado Reservoir only one year pre-invasion (1995). No largemouth bass length-weight data were collected at Clinton Reservoir in 1993, 1995, and 2007-2008, and at El Dorado Reservoir in 1995 and 2008. Mean relative weight of largemouth bass ranged from 78.19 (SE = 7.02; Clinton 1999) to 101.50 (SE = 3.40; El Dorado 2002), and did not differ between reservoirs across time (*P*s > 0.363; Figure 2.2; Tables 2.3, 2.4, 2.5). No walleye length-weight data were collected from El Dorado Reservoir in 1995-1996. Mean relative weight of walleye ranged from 80.44 (SE = 1.56; Milford 2000) to 132.53 (SE = 12.35; Marion 1995), but did not differ between El Dorado Reservoir and the control reservoirs across time (*P*s > 0.408; Figure 2.2; Tables 2.3, 2.4, 2.5). No length-weight data were collected for white bass in El Dorado Reservoir in 1996. Mean relative weight of white bass ranged from 65.78 (SE = 7.12; Milford 1997) to 107.00 (SE = 1.79; Marion 2008). However, mean relative weight of white bass in El Dorado Reservoir declined from 98.59 (SE = 0.81) during the pre-invasion period to 88.42 (SE = 0.87) during the post-invasion period (10% decline), while mean relative weight of white bass declined by an average of 1% in control systems (*P*s < 0.001; Figure 2.2; Tables 2.3, 2.4, 2.5). No white crappie length-weight data were collected from Clinton Reservoir in 2004, El Dorado Reservoir in 1997 and 2008, and Marion Reservoir in 1994 and 1997. Mean relative weight of white crappie ranged from 70.69 (SE = 3.31; Milford 1996) to 132.40 (SE = 40.76; Marion 1995). However, mean relative weight of white crappie in El Dorado Reservoir declined from 91.05 (SE = 1.17) during the pre-invasion period to 86.66 (SE = 1.66) during the post-invasion period (5% decline), while mean relative weight of white crappie increased by an average of 11% in control systems (*P*s < 0.081; Figure 2.2; Tables 2.3, 2.4, 2.5).

Therefore, condition of bluegill, white bass, and white crappie in El Dorado Reservoir all declined more than control reservoirs after zebra mussel invasion.

Discussion

Our results generally did not support our hypothesis that adult fish abundance would decline following zebra mussel invasion. However, our results indicated that condition of bluegill, white bass, and white crappie in El Dorado Reservoir declined following zebra mussel invasion, in comparison to similar control reservoirs over the same time period. These results indicate the possibility that zebra mussel presence may affect the condition of some reservoir fish species in the Great Plains.

Bluegill, gizzard shad, largemouth bass, walleye, and white bass exhibited no change in abundance following zebra mussel invasion in El Dorado Reservoir, and white crappie abundance remained relatively consistent in El Dorado Reservoir following zebra mussel invasion in comparison to declines in the control reservoirs. These findings may be attributable to other factors affecting fish abundance, such as reservoir hydrology and stocking (Slipke et al. 1998; Schultz et al. 2002; Quist et al. 2004; Colvin et al. 2008). Bluegill mean CPUE was less than 6 fish per trap net in 86% of yearly samples, but was affected by outliers (Milford and Marion each had two years with mean CPUE >12, with one year as high as 67.81) and high variability among reservoirs, which contributed to the lack of statistical significance of our results. The lack of response from gizzard shad was likely due to extensive year-to-year variability in abundance, as well as an opportunistic diet that is composed primarily of zooplankton during larval stages and detritus and phytoplankton during their adult lives (Stein et al. 1995; Schultz et al. 2002). Larval gizzard shad can transition to phytoplankton and detritus if their preferred zooplankton prey becomes limited (Dettmers and Stein 1996; Miranda and Gu 1998). Thus, if zebra mussel invasion in El Dorado Reservoir was associated with declines in zooplankton abundance, gizzard shad may have shifted their diets in response, mitigating impacts on abundance or growth. Many reservoir fish species including largemouth bass, walleye, white bass, and white crappie often exhibit considerable population variability related to the population characteristics of forage fish (age-0 bluegill and gizzard shad), reservoir water levels, water temperature, and a variety of other factors (Stein et al. 1995; Slipke et al. 1998; Parkos and Wahl 2002; Willis et al. 2002; Quist et al. 2004). Although our analysis accounted for variable reservoir water levels, continued analysis of long-term data may provide additional insights on the effects of zebra mussels on reservoir fish abundance.

The reduced condition of bluegill, white bass, and white crappie in El Dorado Reservoir following zebra mussel invasion supported our hypothesis that condition of reservoir fishes may decline following zebra mussel invasion. This response may be related to food shortages early in life that continue to influence fish older than age-0. Larval bluegill, gizzard shad, largemouth bass, walleye, white bass, and white crappie all depend on zooplankton as a primary food source (Stein et al. 1995; Dettmers and Stein 1996; Miranda and Gu 1998; Bremigan and Stein 2001; Willis et al. 2002; Quist et al. 2004; Strakosh et al. 2009). Thus, if zebra mussel invasion led to a reduction in zooplankton in El Dorado Reservoir, these six species may have experienced food shortages at age-0, leading to reduced condition. In addition, if age-0 fishes decline in abundance due to food shortages, this would lead to food shortages for adult piscivores, resulting in a possible decline in abundance or condition of these adult fishes.

Richardson and Bartsch (1997) found no effect on the growth of age-0 bluegill (34-mm mean total length) contained in mesocosms with zebra mussels in comparison to age-0 bluegill kept in control mesocosms, and hypothesized this was due to bluegill switching from zooplankton to macroinvertebrate food sources to supplement their diets when zooplankton was limited. However, Harris et al. (1999) found that up to 92% of adult bluegill (>79-mm total length) diets in a South Dakota impoundment were composed of zooplankton at various times during the year, suggesting that low zooplankton abundance may continue to affect adult bluegill condition. In addition, age-0 white crappie may transition to macroinvertebrates and fish as prey later in the fall than other piscivores, leaving them vulnerable to zooplankton shortages for a longer period of time (Miranda and Gu 1998). Age-0 white bass also depend heavily upon zooplankton (Schultz et al. 2002). Preigel (1970) found that zooplankton was the primary dietary component of age-0 white bass in Lake Winnebago, Wisconsin, from June-October of their first year of life, and piscivory was not an important component of white bass diets until fish reached at least 188 mm. Therefore, reduced condition of these reservoir fishes may be linked to limited food availability due to zebra mussel invasion.

Fish stocking may be a possible explanation for the lack of response in abundance and condition of largemouth bass and walleye. Because both species depend on zooplankton in larval stages (Mathias and Li 1982; Olson 1996), a response in condition similar to that observed for bluegill, white bass, and white crappie was expected. However, largemouth bass and walleye are both popular sportfish with reservoir populations that are regularly supplemented with stocking by Kansas Department of Wildlife and Parks. El Dorado Reservoir was stocked with an average of over 2,000,000 largemouth bass and over 28,000,000 walleye per year between 2004-2006 (J. Goeckler, KDWP, unpublished data). This stocking may mask a response to zebra mussel invasion.

Additional research into the effects of zebra mussels on fish populations in warm-water reservoirs is needed to determine the mechanisms of the effects of zebra mussels on reservoir fishes. Our correlative results suggest that declines in reservoir fish condition were associated with the presence of zebra mussels in El Dorado Reservoir. However, our study did not identify the mechanism for these declines, and it is important to note that zebra mussel abundance has varied substantially in El Dorado Reservoir during the five post-zebra mussel invasion years of our study. Mean summer (June-August) zebra mussel veliger densities, which KDWP uses as an index of zebra mussel abundance, were less than 5 veligers/L in 2004 and 2008, and peaked at over 115 veligers/L in 2006 (See Appendix B.3; J. Goeckler, KDWP, unpublished data). In addition, summer water temperatures and turbidity in El Dorado Reservoir frequently exceed the thermal and turbidity optima of zebra mussels (17-23° C, 40-200 cm Secchi disc; Ludyanskiy et al. 1993), and the combination of high temperature and turbidity exerts considerable stress upon zebra mussels, though zebra mussels in chronically warm and turbid systems may be able to acclimate over time (Alexander et al. 1994). Continued monitoring of trends in zebra mussel abundance and fish abundance and condition in El Dorado Reservoir and the control reservoirs may be necessary to more fully understand the effects of zebra mussel invasion. In addition to predicted effects upon zooplankton, zebra mussel invasion may also affect macroinvertebrate communities (Ricciardi et al. 1997; Stewart et al. 1998), and macroinvertebrates are a common transition prey item for piscivores undergoing ontogenetic niche shifts from zooplanktivory to piscivory (Mathias and Li

1982; Olson 1996; Willis et al. 2002). Thus, changes in macroinvertebrate communities may be another mechanism by which zebra mussels could influence fish abundance and condition. Diet analysis of young-of-the-year piscivores in warm-water systems invaded by zebra mussels and zebra mussel-free systems, including analysis of zooplankton, macroinvertebrate, and fish abundance in diets, may provide a better understanding of the mechanism of zebra mussel effects on fishes. Continued research and monitoring will be necessary to understand the responses of reservoir fish communities to zebra mussel invasion in warm-water systems like those in the Great Plains and the Southwest, and to provide reservoir managers with the information necessary to manage fish communities in zebra mussel-infested reservoirs.

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Table 2.1 Hydrologic characteristics of El Dorado Reservoir (zebra mussel system) and Clinton, Marion, and Milford reservoirs (control systems). Data obtained from Kansas Biological Survey (2010).

	El Dorado Reservoir	Clinton Reservoir	Marion Reservoir	Milford Reservoir
River Basin	Walnut	Kansas-Lower Republican	Neosho	Kansas-Lower Republican
Watershed Drainage Area (km^2)	606	951	518	9832
Completion Date	1981	1977	1968	1967
Conservation Pool Top Elevation (m)	408.1	266.9	411.0	348.8
Zebra Mussel Establishment	2003	NA	Summer 2008	NA
Surface Area (ha)	3237	2833	2943	6483
Mean Depth (m)	3.3	5.2	4.0	7.4
Maximum Depth (m)	18.3	16.8	9.3	19.8
Residence Time (years)	1.0	0.8	2.0	1.0

Table 2.2 Mean catch per unit effort of six species of stock-to-quality length fish in El Dorado Reservoir (zebra mussel invaded reservoir) and Clinton, Marion, and Milford reservoirs (control reservoirs) from 1993-2002 (pre-invasion period) and 2004-2008 (post-invasion period). Largemouth bass sampling occurred in El Dorado and Clinton reservoirs only. *P*-values test if trends in mean CPUE were consistent between El Dorado Reservoir and the control reservoirs in the pre- and post-zebra mussel invasion periods. *P*-values were plural because four tests were conducted for each species with seasonal water levels as covariates (see Table 2.5); SE=standard error.

	1993-2002		2004-2008	
Species and Reservoir	Mean	SE	Mean	SE
Bluegill (fish per trap net; *P*s > 0.528)				
El Dorado	1.28	0.32	2.94	0.50
Clinton	2.90	0.39	4.28	0.92
Marion	3.76	1.32	3.47	1.40
Milford	10.04	5.68	4.54	0.83
Gizzard Shad (fish per gill net; *P*s > 0.158)				
El Dorado	2.32	1.20	1.24	0.31
Clinton	9.70	1.79	4.02	1.44
Marion	9.89	2.62	3.90	1.25
Milford	8.23	1.55	1.77	0.87
Largemouth Bass (fish per electrofishing hour; *P*s > 0.154)				
El Dorado	3.75	0.44	5.79	1.05
Clinton	1.70	0.33	2.80	0.64
Walleye (fish per gill net; *P*s > 0.258)				
El Dorado	1.96	0.33	2.47	0.43
Clinton	1.33	0.20	1.02	0.32
Marion	1.94	0.31	1.63	0.38
Milford	1.26	0.22	1.90	0.34
White Bass (fish per gill net; *P*s > 0.415)				
El Dorado	6.61	1.75	1.07	0.33
Clinton	8.21	2.29	13.65	3.62
Marion	16.08	3.16	5.42	1.45
Milford	2.38	0.68	1.57	0.52
White Crappie (fish per trap net; *P*s < 0.028)				
El Dorado	2.68	0.41	2.07	0.46
Clinton	17.09	1.54	6.59	1.39
Marion	7.02	2.54	2.10	0.56
Milford	4.91	0.95	0.86	0.21

Table 2.3 Mean relative weight of five species of stock-to-quality length fish (gizzard shad omitted because of insufficient pre-invasion data) in El Dorado Reservoir (zebra mussel invaded reservoir) and Clinton, Marion, and Milford reservoirs (control reservoirs) from 1993-2002 (pre-invasion period) and 2004-2008 (post-invasion period). Largemouth bass sampling occurred in El Dorado and Clinton reservoirs only. *P*-values test if trends in mean relative weight were consistent between El Dorado Reservoir and the control reservoirs in the pre- and post-zebra mussel invasion periods. *P*-values were plural because four tests were conducted for each species with seasonal water levels as covariates (see Table 2.5); SE=standard error.

	1993-2002		2004-2008	
Species and Reservoir	Mean	SE	Mean	SE
Bluegill (*P*s < 0.002)				
El Dorado	104.09	1.99	95.63	1.29
Clinton	93.39	1.52	98.99	1.73
Marion	94.10	1.18	101.31	9.19
Milford	102.83	2.94	101.89	2.62
Largemouth Bass (*P*s > 0.363)				
El Dorado	92.39	0.62	94.38	1.97
Clinton	91.05	1.08	97.54	1.86
Walleye (*P*s > 0.408)				
El Dorado	90.86	0.60	88.87	0.82
Clinton	91.64	0.66	90.59	1.21
Marion	94.71	0.78	92.51	1.18
Milford	92.60	1.04	93.81	0.92
White Bass (*P*s < 0.001)				
El Dorado	98.59	0.81	88.42	0.87
Clinton	97.40	0.72	93.81	0.59
Marion	100.41	0.35	94.43	1.31
Milford	87.38	1.06	92.80	0.99
White Crappie (*P*s < 0.081)				
El Dorado	91.05	1.17	86.66	1.66
Clinton	88.21	0.69	87.96	1.88
Marion	85.51	1.44	97.54	2.80
Milford	92.41	0.97	108.76	3.57

Table 2.4 Percent change in mean catch per unit effort (fish per gill net [GN], trap net [TN], or electrofishing hour [EF]) and relative weight of six species of stock-to-quality length fish (gizzard shad omitted from relative weight calculations because of insufficient data) in El Dorado Reservoir (invaded reservoir) and Clinton, Marion, and Milford reservoirs (control reservoirs) between the pre-invasion time period (1993-2002) and the post-invasion time period (2004-2008). Largemouth bass sampling occurred in El Dorado and Clinton reservoirs only. *Indicates a significant contrast *P*-value—trends in mean CPUE or relative weight differ between El Dorado Reservoir and the control reservoirs in the pre- and post-zebra mussel invasion periods.

		Control Reservoirs			
Species	El Dorado	Mean	Clinton	Marion	Milford
CPUE					
Bluegill [TN]	+130%	-5%	+48%	-8%	-55%
Gizzard Shad [GN]	-47%	-66%	-59%	-61%	-78%
Largemouth Bass [EF]	+54%		+65%		
Walleye [GN]	+26%	+4%	-23%	-16%	+51%
White Bass [GN]	-84%	-11%	+66%	-66%	-34%
White Crappie [TN]*	-23%	-71%	-61%	-70%	-82%
Relative Weight					
Bluegill*	-8%	+4%	+6%	+8%	-1%
Largemouth Bass	+2%		+7%		
Walleye	-2%	-1%	-1%	-2%	+1%
White Bass*	-10%	-1%	-4%	-6%	+6%
White Crappie*	-5%	+11%	0%	+14%	+18%

Table 2.5 Covariate (Cov *P*) and contrast (Con *P*) *P*-values testing whether trends in abundance (top) of six species and relative weight (bottom) of five species (gizzard shad omitted due to insufficient data) of stock-to-quality length differ between El Dorado Reservoir and the control reservoirs before and after zebra mussel invasion, using mean water level deviation from conservation pool for each reservoir in spring (March-May), summer (June-August), fall (September-November), and winter (December-February) as covariates. A contrast *P*-value less than 0.05 (bolded) indicated that trends differed between El Dorado Reservoir and the control reservoirs over time.

	Spring		Summer		Fall		Winter	
	Cov *P*	Con *P*	Cov *P*	Con *P*	Cov *P*	Con *P*	Cov *P*	Con *P*
Abundance (CPUE) *P*-values								
Bluegill	0.028	0.529	0.641	0.559	0.846	0.558	0.237	0.685
Gizzard Shad	0.122	0.223	0.229	0.159	0.825	0.200	0.207	0.163
Largemouth Bass	0.623	0.550	0.003	0.155	0.032	0.238	0.655	0.408
Walleye	0.983	0.314	0.174	0.259	0.077	0.383	0.397	0.284
White Bass	0.028	0.416	0.920	0.498	0.228	0.551	<0.001	0.672
White Crappie	<0.001	**0.023**	0.008	**0.012**	0.173	**0.027**	<0.001	**0.001**
Relative Weight (W_r) *P*-values								
Bluegill	0.008	**0.001**	0.009	**0.001**	<0.001	**<0.001**	0.024	**<0.001**
Largemouth Bass	0.286	0.539	0.138	0.364	0.043	0.393	0.001	0.685
Walleye	0.771	0.524	0.013	0.409	<0.001	0.571	0.483	0.526
White Bass	<0.001	**<0.001**	<0.001	**<0.001**	<0.001	**<0.001**	<0.001	**<0.001**
White Crappie	<0.001	**0.049**	0.007	0.080	0.215	**0.041**	0.068	**0.015**

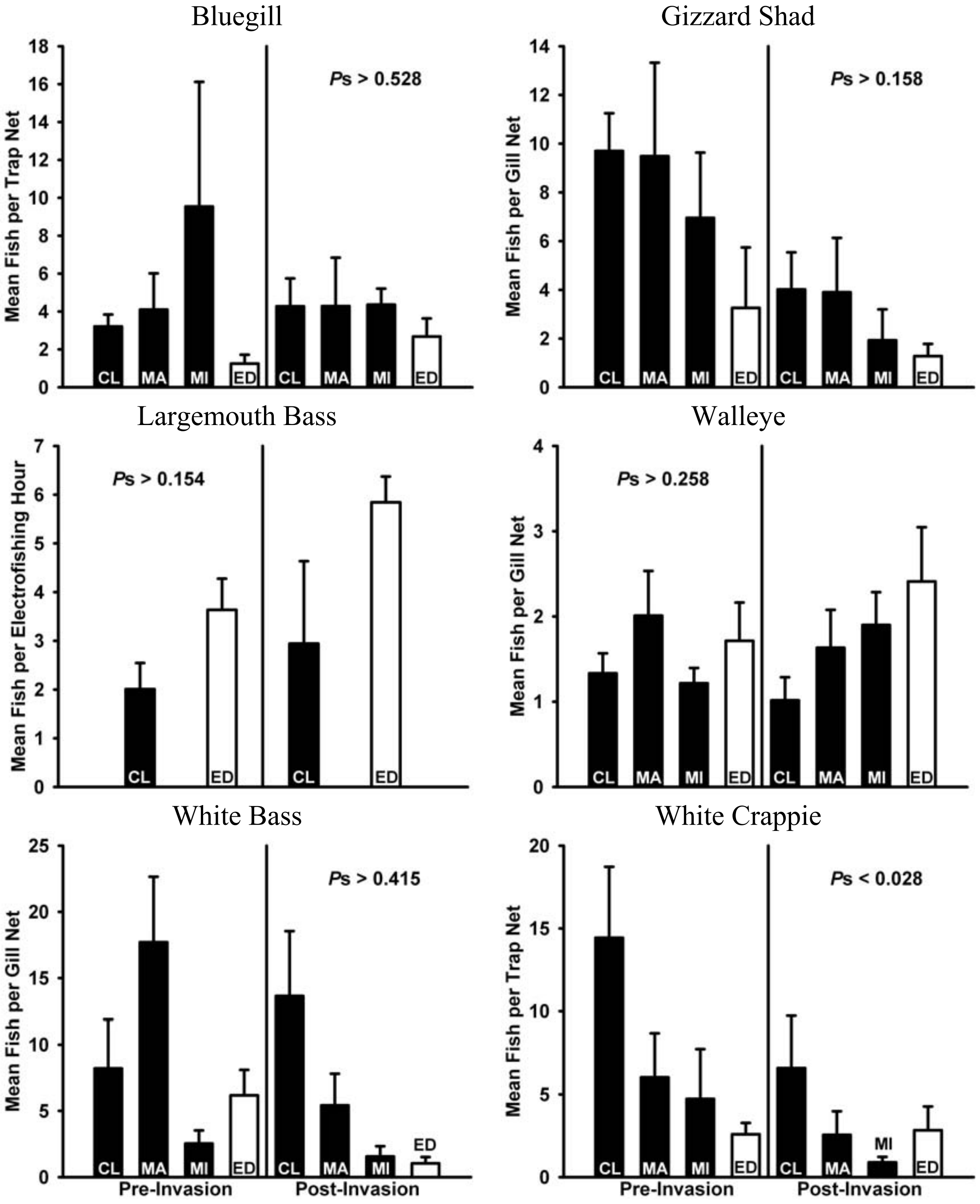


Figure 2.1 Mean pre-invasion (1993-2002) and post-invasion (2004-2008) catch per unit effort (CPUE) of stock-to-quality length bluegill, gizzard shad, largemouth bass, walleye, white bass, and white crappie collected during fall standardized sampling using gill nets (gizzard shad, walleye, white bass), trap nets (bluegill, white crappie), and electrofishing (largemouth bass). Error bars represent one standard error; contrast *P*-values test if trends in mean CPUE were consistent between El Dorado Reservoir and the control reservoirs in the pre- and post-zebra mussel invasion periods. CL = Clinton Reservoir, MA = Marion Reservoir, MI = Milford Reservoir, and ED = El Dorado Reservoir.

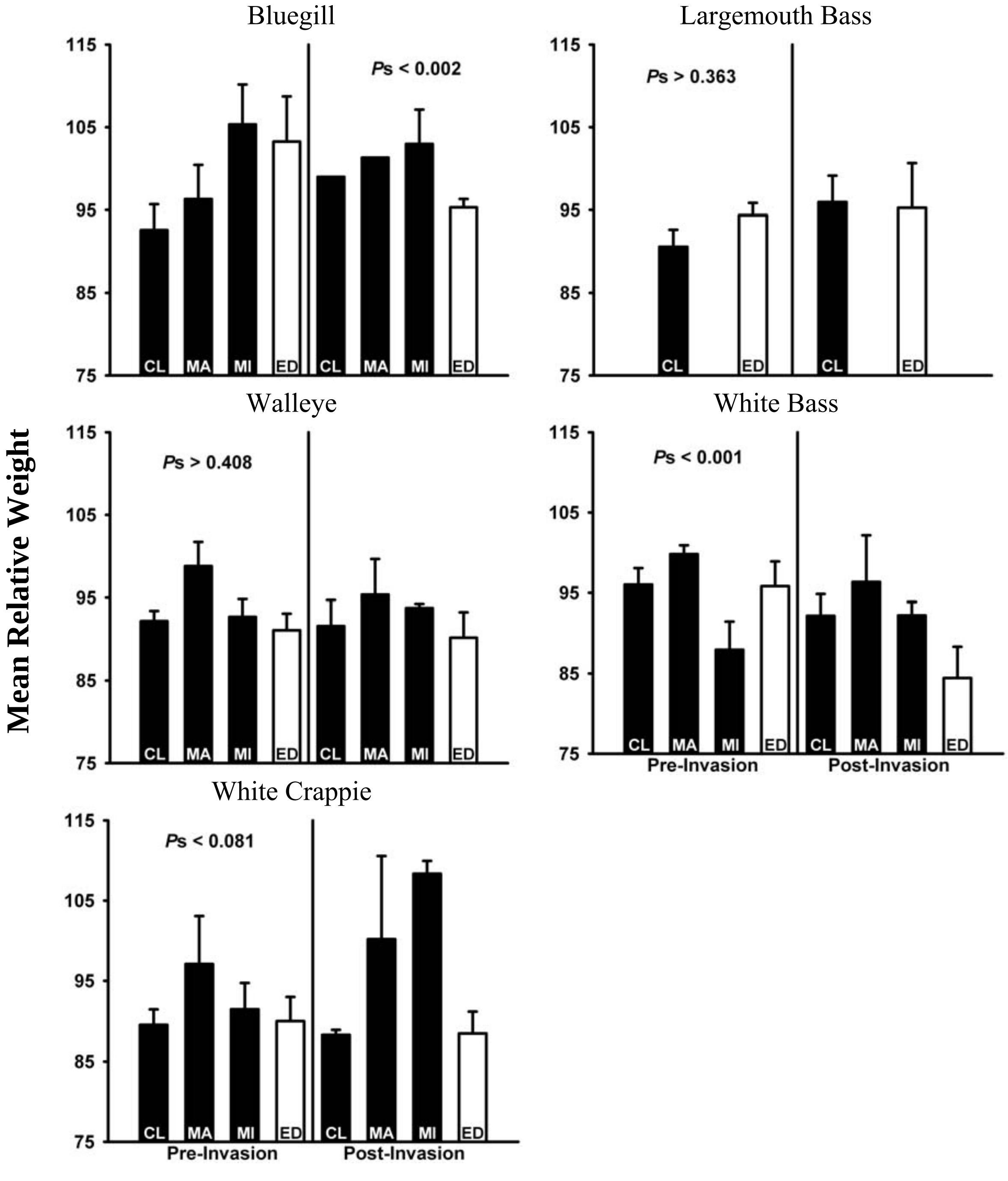


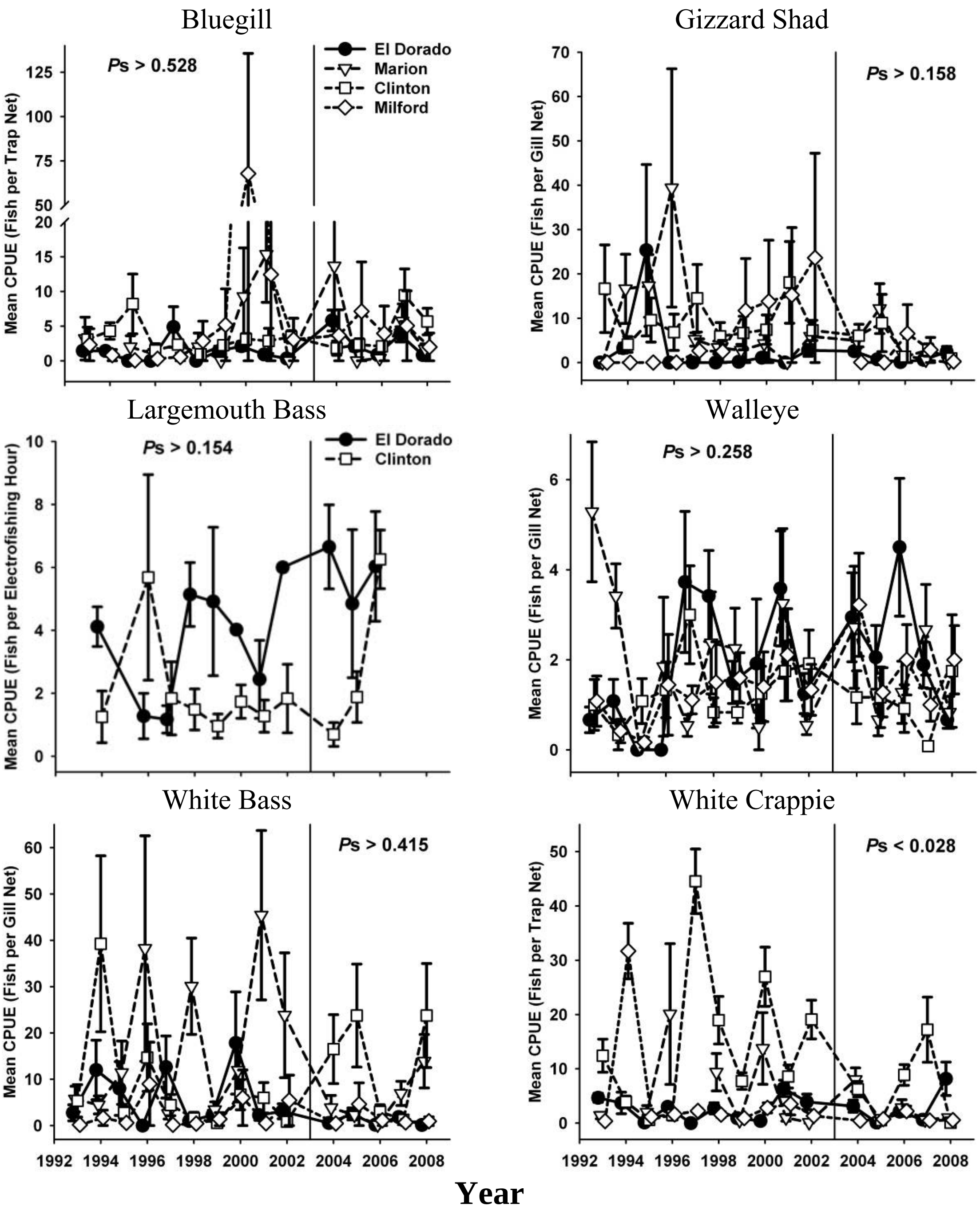
Figure 2.2 Mean pre-invasion (1993-2002) and post-invasion (2004-2008) relative weight of stock-to-quality length bluegill, largemouth bass, walleye, white bass, and white crappie collected during fall standardized sampling (gizzard shad omitted because of insufficient data). Error bars represent one standard error; contrast *P*-values test if trends in mean relative weight were consistent between El Dorado Reservoir and the control reservoirs in the pre- and post-zebra mussel invasion periods. CL = Clinton Reservoir, MA = Marion Reservoir, MI = Milford Reservoir, ED = El Dorado Reservoir.

Appendix A - Chapter 1 Supplement

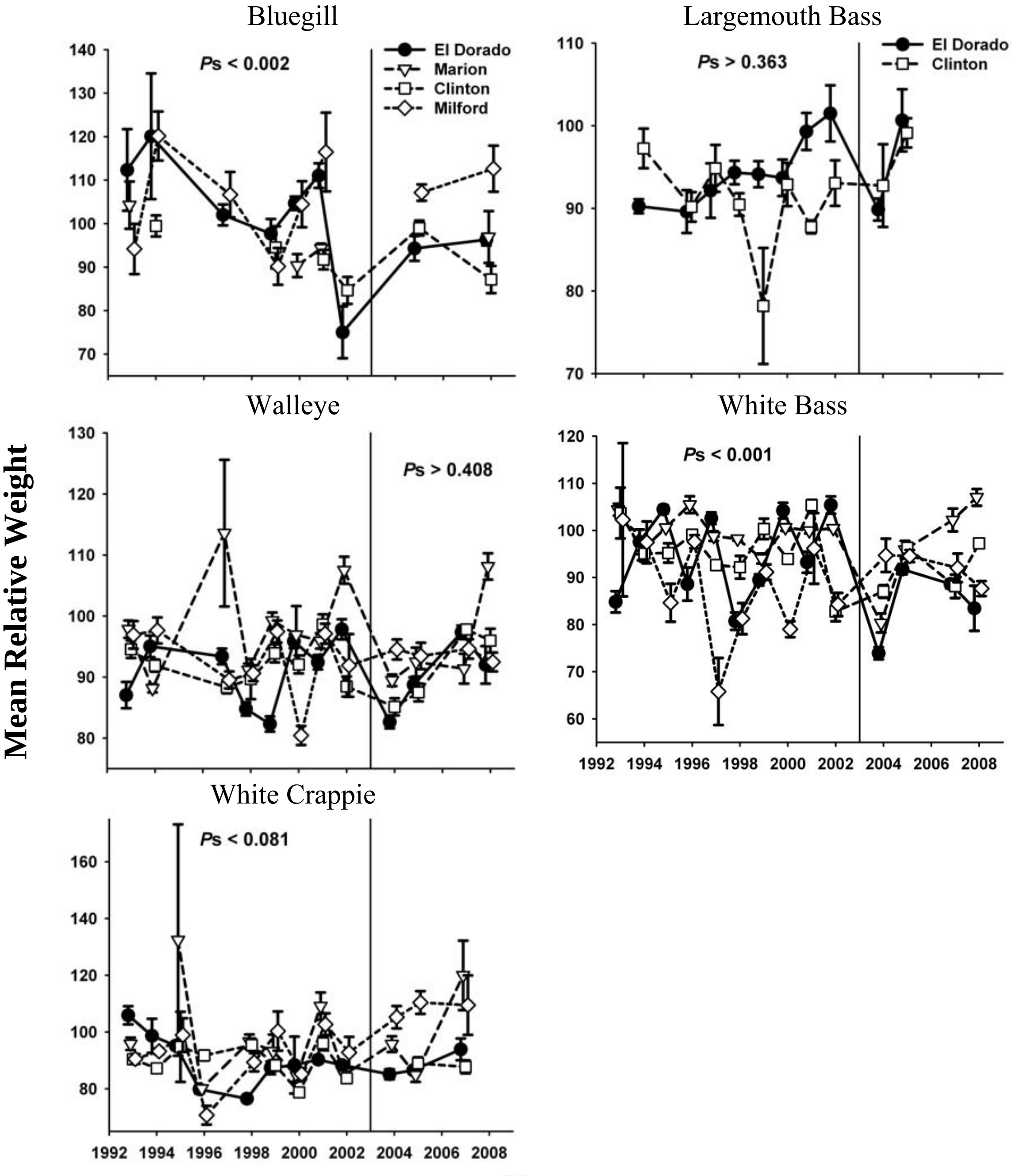
Appendix A.1 Mean habitat measurements for El Dorado and Melvern reservoirs in the pre-zebra mussel invasion period (2001-2002) and the post-zebra mussel invasion period (2008-2009). Water temperature, dissolved oxygen, turbidity, conductivity, and vegetation densities were measured in sampling enclosures. Mean zebra mussel veliger densities were calculated from lake-wide data provided by J. Goeckler, Kansas Department of Wildlife and Parks. ED = El Dorado Reservoir (zebra mussels), MV = Melvern Reservoir (control).

	Pre-Invasion				Post-Invasion			
	2001		2002		2008		2009	
	ED	MV	ED	MV	ED	MV	ED	MV
Mean Water Temperature (°C)	29.6	31.8	26.9	29.9	27.6	30.2	29.1	28.2
Mean Dissolved Oxygen (mg/L)	5.6	4.4	7.5	7.6	6.3	7.9	6.6	7.3
Mean Turbidity (NTU)	61.9	6.1	42.1	22.6	93.5	206.5	100.3	61.5
Mean Conductivity (µs/cm)	288	339	286		212	307	223	310
Mean Water Willow Density (stems/m^2)	2.8	6.1	1.6	0.0	1.0	2.4	0.3	0.0
Mean Total Vegetation Density (stems/m^2)	4.1	50.4	1.6	1.9	2.6	4.0	0.3	0.0
Mean July-August Zebra Mussel Veliger Density (number/L)					1.0		0.3	

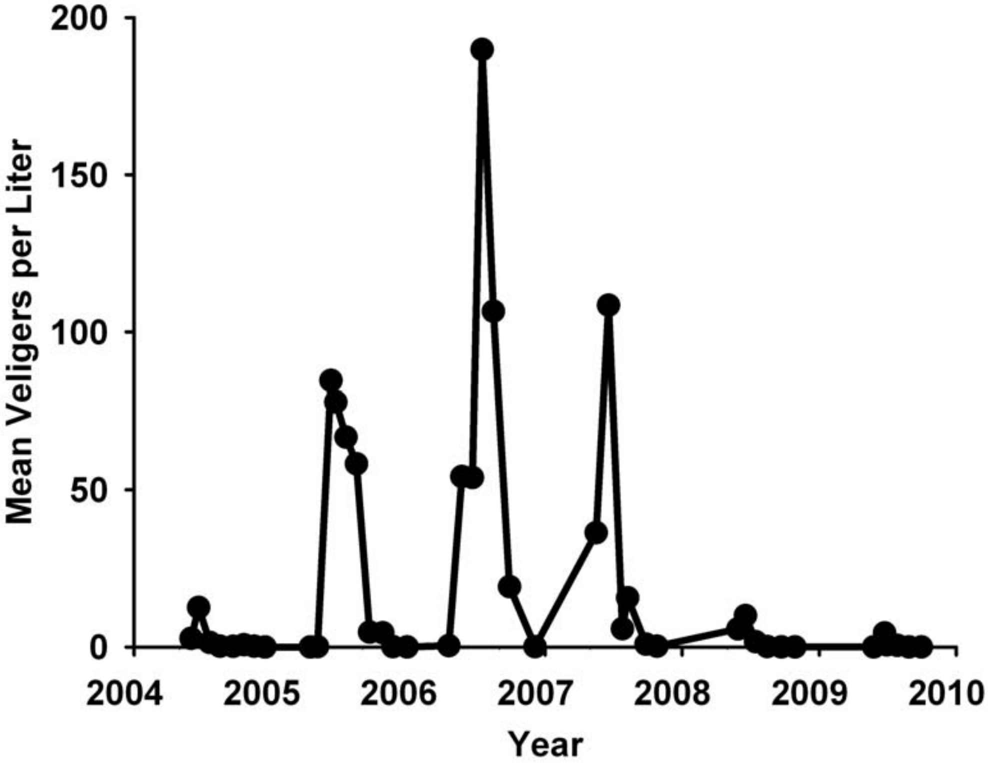
Appendix B - Chapter 2 Supplement



Appendix B.1 Mean catch per unit effort (CPUE) of stock-to-quality length bluegill, gizzard shad, largemouth bass, walleye, white bass, and white crappie collected during fall standardized sampling using gill nets (gizzard shad, walleye, white bass), trap nets (bluegill, white crappie), and electrofishing (largemouth bass). Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. Contrast *P*-values test if trends in mean CPUE were consistent between El Dorado Reservoir and the control reservoirs in the pre- and post-zebra mussel invasion periods.



Appendix B.2 Mean relative weight of stock-to-quality length bluegill, largemouth bass, walleye, white bass, and white crappie collected during fall standardized sampling (gizzard shad omitted because of insufficient data). Vertical bar indicates year of zebra mussel invasion (2003); error bars represent one standard error. Contrast *P*-values test if trends in mean relative weight were consistent between El Dorado Reservoir and the control reservoirs in the pre- and post-zebra mussel invasion periods.



Appendix B.3 Mean zebra mussel veliger density (number/L) in El Dorado Reservoir from 2004 to 2009. Data collected from several reservoir locations by J. Goeckler and C. Johnson, Kansas Department of Wildlife and Parks.