INFLUENCES OF BIOLOGICAL VEGETATION CONTROL ON SPORT FISH CHARACTERISTICS AND AQUATIC PLANT COMMUNITIES IN SOUTHERN ARKANSAS

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ABSTRACT

In approximately 2000, hydrilla *Hydrilla verticillata* was found in Felsenthal National Wildlife Refuge (FNWR). By 2004, hydrilla and other submerged vegetation began limiting recreational areas by declining open water in prime fishing locations. The increase of hydrilla and other nuisance submerged vegetation led to a reduction in angler visits. In the fall of 2008, the Arkansas Game and Fish Commission and the U.S. Fish and Wildlife Service initiated a joint large-scale nuisance submerged vegetation project, where approximately 150,000 triploid grass carp *Ctenopharyngodon idella* were stocked into FNWR.

In this study, we monitored vegetation percent coverage, biomass, and community composition in response to grass carp stockings. One year of pre-stocking data was collected during 2008 with 2 years of post-stocking data collected during 2009 and 2010. The refuge was divided into three parts - designated north, east, and west. The north part consisted of all areas in the refuge north of U.S. Highway 82. The east and west parts were south of Highway 82, and were separated by the main channel of the Ouachita River. Aquatic vegetation percent cover, biomass, and community composition were assessed at 23 locations throughout the FNWR using 69, 20-m transects and 1-m^2 quadrats. Ten exclusion cages throughout the refuge were used to estimate production of submerged vegetation, and to determine control feasibility of grass carp. Grass carp annual individual consumption were modeled at maximum, median, and minimum observed weight gains using literature conversion ratios and the Wisconsin Bioenergetics Model. Bluegill and largemouth bass populations characteristics were assessed at 21 locations throughout FNWR using 42, 10-min DC electrofishing transects.

Percent coverage of aquatic vegetation increased after the stocking of grass carp. Mean (SD) percent coverage was 11.5% (28.7) and 33.3% (45.8) in 2008 and 2010, respectively. There was a difference in percent coverage among parts of the refuge. The percent coverage declined in north part and increased in the east and west part. The Wilcoxon rank sums test indicated percent coverage significantly differed between years with 2010 being higher than 2008. The percent similarity index based on percent coverage data indicated a 58% similarity in vegetation communities between years.

Biomass of aquatic vegetation also increased after the stocking of grass carp. Mean biomass was 57.8 (157.2) g/m^2 and 138.1 (346.5) g/m^2 in 2008 and 2010, respectively. There was a difference in biomass among parts. The percent coverage declined in north part and increased in the east and west part. The interaction was significant for mean hydrilla biomass. Hydrilla biomass declined in the east and the west part and was unchanged in the north part. There was no significant difference in American lotus biomass. Percent similarity based on biomass data indicated only a 42% similarity in vegetation communities between years.

American lotus, hydrilla, egeria, coontail, and duckweed dominated the vegetation community before grass carp stocking, based on biomass. The vegetation community after grass carp stocking, based on biomass, was dominated by American lotus, fragrant water lily *Nymphaea odorata*, coontail, duckweed, and hydrilla.

Vegetation biomass differed between inside and outside exclusion cage samples. Hydrilla biomass was significantly different between inside and outside samples. Average hydrilla biomass was almost 500 times greater in samples from inside exclusion cages. American lotus biomass did not differ significantly between inside and outside samples.

Total biomass differed significantly between samples inside and outside the exclusion cages. Total vegetation was greater inside the exclusion cages compared to that observed outside the exclusion cages. Percent coverage and biomass increased in 2010 compared to 2008. However, the increase in percent coverage and biomass was due to an increase in American lotus and fragrant water lily in 2010. Whereas, hydrilla and all other submerged vegetation declined in percent coverage and biomass.

An obvious decline in hydrilla biomass was observed during this study after stocking grass carp. Grass carp virtually eliminated both native and nonnative submerged vegetation. Elimination of submerged vegetation in FNWR led to a major shift in the aquatic vegetation community. The system shifted from a system dominated by submerged vegetation to a system dominated by emergent and floating vegetation.

Modeling grass carp annual individual consumption was within an order of magnitude for both methods. Annual individual consumption using literature values were 284,726, 125,386, and 50,256 g vegetation/year. Annual individual consumption using the bioenergetic method indicated consumption was 150,990, 148,650, and 151,912 g vegetation/year. The conversion ratio method produced the highest and lowest annual individual consumption estimates. All estimates of annual individual consumption using the bioenergetic method were within the range of values produced by the conversion ratio method. Consumption estimates using bioenergetics modeling indicated the number of grass carp stocked between 2008 and 2009 could have easily controlled hydrilla production in FNWR. The difference in hydrilla biomass inside and outside of the exclusion cages supports the assertion that grass carp consumption controlled hydrilla production. Despite the uncertainties associated conversion ratios from the literature, and parameters in the bioenergetics model, grass carp consumption could easily account for more than 11 times the median observed hydrilla production.

Changes in sportfish population characteristics were evident following control of submerged vegetation in FNWR. Bluegill and largemouth bass CPUE in FNWR moderately increased over the study. Largemouth bass and bluegill W_r varied in FNWR throughout our study. However, mean W_r for both species were lowest in 2010. Bluegill PSD and PSD-P varied during our study, with no clear trends through time in any of the parts. Largemouth bass mean PSD and PSD-P were higher in 2008 than 2009 and 2010. Although, bluegill and largemouth bass population characteristic changes were evident following the control of submerged vegetation, discerning the cause and effect of these changes is near impossible.

Variations in water levels in FNWR through time and grass carp consumption were likely equally responsible for reduction in submerged vegetation. Discerning differences between the effects of the high water and the effects of grass carp consumption were not important for this study. More important was that submerged vegetation control improved access to FNWR for recreational user groups, thus, increasing fishing visitors by 63% compared to years before grass carp stocking.

DEDICATION

This thesis dedicated to my grandfather Bert Alvin Timmons and my best friend Joseph Itchimatsu Williams. First to my grandfather, besides bestowing on me your initials, I thank you for teaching me to fish and giving me my first fishing pole, the classic Zebco 303 combo. Without your love and encouragement, I would not be the man I am today. To Joey, thank you for inspiring my return to school. You showed me that it is never too late to resurrect yourself from the ashes. Everybody was Kung Fu Fighting!

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Introduction

An overabundance of aquatic vegetation results in negative ecological and socio-economic consequences for many lake and reservoir ecosystems (Colle et al. 1987). Felsenthal National Wildlife Refuge (FNWR) experienced a reduction in angler visits due to high levels of nuisance aquatic vegetation reducing open water in prime fishing locations. In the 1990s, angler visits to FNWR exceeded 500,000 annually. However, there was a 66% reduction of angler visits between 2004 and 2007. Angler visits fell to approximately 200,000 annually, which is striking considering the size and popularity of the refuge (Williams 2009). The decline in angler visitors to FNWR predictably decreased sportfishing revenue for Ashley, Bradley, and Union counties (Williams 2009). Declines in angler visitation to FNWR were believed directly related to the expansion of nuisance aquatic vegetation (Williams 2009). Vegetation was not regarded as a problem before the early 1990s. However, by the late 1990s, various littoral plant species began to spread rapidly throughout the refuge. Olive and Thurman (2007) estimated that 90% of backwaters within FNWR had been captured by aquatic vegetation. However, more quantitative estimates of percent coverage, biomass, and community composition had not been attempted prior to the present study.

Problems resulting from aquatic vegetation can be multidimensional. Invasive nuisance vegetation can lead to a reduction of native plant biodiversity and disrupt natural ecosystem processess (Ramey 2002). Native vegetation is an integral part of an aquatic ecosystem and is important to both fish and wildlife (Colle and Shireman 1980). Aquatic vegetation that exceeds moderate densities (> 30% areal coverage) reduces habitat quality for fishes (Ramey 2002), complicates the angling experience (Bain and Boltz 1992), and impedes navigation (Allen and Tugend 2002; Allen et al. 2003). For example, hydrilla *Hydrilla verticillata* coverage on Orange Lake, Florida nearly eliminated bluegill *Lepomis macrochirus*, redear sunfish *L. microlophus,* and black crappie *Pomoxis nigromaculatus* fisheries (Colle et al. 1987). Disruption of the natural ecosystem can lead to unpredictable shifts in community structure of fish species, and thus, interrupt the natural balance of predator-prey relationships.

Largemouth bass *Micropterus salmoides* and bluegill populations are generally managed to maintain a "balanced" predator-prey relationship. Such balanced predator-prey relationships usually result in long-term, quality sportfishing that provides harvestable sized individuals of both species (Swingle 1956). However, high levels of nuisance aquatic vegetation can influence this predator-prey balance. Expansive aquatic vegetation stands can alter feeding efficiency of sportfishes, and thus, reduce their first-year growth (Bettoli et al. 1992). Communities of prey fish rely on moderate coverage of aquatic vegetation (< 30%) for forage and protection. Alternatively, dense hydrilla beds provide too much protection for prey fishes, and contribute to stunted fish populations and unbalanced communities (Colle and Shireman 1980). For instance, sunfish communities tend to be dominated by small and intermediate-sized individuals in conditions of overabundant aquatic vegetation (Bettoli et al. 1992). Furthermore, when aquatic vegetation becomes overabundant, habitat complexity increases reducing feeding efficiency and growth in largemouth bass (Bettoli et al. 1992).

Chemical, biological, and mechanical methods have been employed to control native and invasive aquatic plants (Harley and Forno 1992). Biological control methods are preferred because they are relatively inexpensive and longer lasting (Beyers and Carlson 1993). Grass carp *Ctenopharyngodon idella* are the most commonly used fish species for biological control of aquatic vegetation in the United States (Chilton and Muoneke 1992). Grass carp are herbivorous, and when stocked at appropriate rates (1-5 fish/ha), have proven extremely effective at controlling or eliminating unwanted aquatic vegetation. The benefits of grass carp stocking may extend more than 7 years (Shireman et al. 1985). Utilizing grass carp as biological control agents for aquatic vegetation can cost as little as US $250/ha (Shireman et al. 1985). Costs associated with the use of herbicides for nuisance submerged aquatic vegetation control can be 6 to 14 times more expensive than using grass carp (Stott et al. 1971; Shireman 1982). Grass carp stocking coupled with the application of herbicide may be the most effective means of controlling overabundant aquatic vegetation (Chilton and Muoneke 1992).

Utilizing grass carp for control of aquatic vegetation can be complicated because grass carp tend to migrate. Within closed systems (e.g., ponds or lakes), grass carp generally migrate throughout the system. In open systems (e.g., rivers or large reservoirs), grass carp can emigrate from the vicinity of the location where they were stocked (Bain et al. 1990; Prentice et al. 1998). If actual densities of grass carp are too low, they are ineffective at controlling vegetation. Studies to determine the usefulness of grass carp to control aquatic vegetation in open systems have yielded varying results (Clapp et al. 1993; Mitzner 1978; Nixon and Miller 1978; Bain et al. 1990; Prentice et al. 1998; Kirk et al. 2001). Areal coverage of vegetation seems to be the primary factor affecting grass carp movements in these studies. Greater fish movement and even emigration were observed in systems with low vegetation densities. However, in both open and closed systems grass carp tend to be more sedentary with high vegetation density (Kirk et al. 2001).

To study grass carp emigration rates in FWNR reservoir, a radio-telemetry study using triploid grass carp was conducted in 2006-2007. The primary goal of the telemetry study was to determine whether grass carp would remain in the FWNR over long-term time scales throughout periods of variable seasonal flows (Olive and Thurman 2007; Olive et al. 2010). A secondary objective was to track dispersion patterns and movement of radio-tagged grass carp over a 344-d period. During the telemetry study, 82% of 48 tagged grass carp remained in the refuge. Two percent migrated upstream and then returned to the refuge. Ten percent of grass carp were located upstream of refuge waters in either the Ouachita or Saline rivers, whereas 6% of the grass carp were never relocated. No fish were located downstream of Felsenthal Lock and Dam. A similar study by Foltz et al. (1994) in Santee Cooper Reservoir, South Carolina indicated that triploid grass carp generally stayed close to the areas containing hydrilla.

The goal of this thesis research was to evaluate the changes in largemouth bass and bluegill populations, and aquatic vegetation in FNWR associated with the stocking of grass carp. The objectives of this study are:

1. To determine CPUE and population characteristics of largemouth bass and bluegill before and after grass carp stocking in FNWR.
2. To determine composition, percent coverage, and biomass of aquatic vegetation before and after grass carp stocking in FNWR.
3. To model bioenergetics of grass carp in FNWR, projecting aquatic vegetation consumption as a function of fish growth.

Literature Review

Population Characteristics of Fishes in Relation to Aquatic Vegetation

Aquatic vegetation growing in the littoral zone influences predator prey interactions, fish behavior, and fish distribution (Hixon 1986). Aquatic vegetation increases prey fish survival by reducing predation encounter rates (Hosn and Downing 1994). For instance, juvenile sunfishes inhabit aquatic vegetation beds for increased availability of forage and avoidance of predators. In the presence of predators, bluegills will select the highest available stem density cover (Savino and Stein 1989; Gotceitas 1990a, 1990b). Werner et al. (1983) reported bluegill movements are inhibited in dense vegetation in the presence of piscivorous fish. Savino and Stein (1982) further demonstrated that sunfish distribution and behavior were modified by both aquatic vegetation stem density and presence of predators. At high stem densities, largemouth bass were unable to capture bluegills because of the inability to find or follow bluegills through dense vegetation (Savino and Stein 1982; Savino and Stein 1989).

Piscivory efficiency is reduced as abundance of aquatic vegetation increases. With increased vegetation abundance, largemouth bass condition (Colle and Shireman 1980) and growth (Strange et al. 1975) are reduced. The expansion of aquatic vegetation reduces piscivory efficiency through decreased foraging efficiency (Colle and Shireman 1980). In the presence of dense aquatic vegetation, largemouth bass will change to an ambush foraging method rather than active pursuit foraging method employed at low aquatic vegetation density (Savino and Stein 1982; Eklov and Diehl 1994). As habitat complexity increases, predation of bluegills by largemouth bass decreases (Savino and Stein 1982).

Aquatic plant beds are important sanctuaries for young fishes. Moderate levels of aquatic vegetation can generate stable prey-predator relationships (Savino and Stein 1982). Submerged aquatic vegetation provides cover for young bluegills and largemouth bass. Growth of young fish increases in moderate to high densities of hydrilla. However, greater fish growth rates are associated with vegetation beds with more edge areas compared to areas with uninterrupted high-density vegetation patches or areas without vegetation (Morrow et al. 1991). Prey fish growth rates are retarded when fishes are confined to vegetation by risk of predation (Persson 1993; Persson and Eklov 1995). The resultant slower growth rate is allegedly due to increased foraging competition among prey fishes confined to aquatic vegetation. Within vegetation sanctuaries, young bluegills exert strong competitive effects on other littoral fishes, including young largemouth bass. Increased survival of young of the year (age-0) centrarchids due to lower predation leads to increased competition and reduction in growth (Osenberg et al. 1987; Nibbelink and Carpenter 1998). Density and survival of centrarchids may also increase as density of vegetation increases (Kilgore et al. 1989). For example, when bluegill outnumber other species, the effects of juvenile bluegills on young of the year largemouth bass is greater than that of other piscivorous species (Olson et al. 1995), thus, altering the predator-prey relationship between largemouth bass and bluegill.

Changes in predator-prey interactions may be evident after vegetation reduction. Colle et al. (1989) reported fish responses to habitat changes was slow. Condition of bluegill generally improves after the removal of excess aquatic vegetation (Bailey 1978;

Shireman et al.1985). Although Bailey (1978) and Shireman et al. (1985) indicated that as sunfish condition increased, they detected no changes in largemouth bass and bluegill abundance after vegetation removal in Arkansas and Florida lakes, respectively. Noble (1986) and Bettoli et al. (1993) reported declines in littoral species and increases in pelagic species in Lake Conroe, Texas. In Lake Marion, South Carolina, Killgore et al. (1998) showed significant increases in mean catch of all species, including bluegill and largemouth bass, after a 40% reduction in hydrilla.

Results of vegetation control projects have been mixed. Most of the systems mentioned above lack the structural complexity of FNWR. The lakes in Florida and Texas were highly developed systems, with little to no natural littoral structure after vegetation removal. Conversely, FNWR is a more natural system, and has substantial submerged and littoral structure. Lake Marion in South Carolina is more similar to FNWR than the other lakes cited. Lake Marion and FNWR are both located at the confluence of two rivers, subject to fluctuations in water levels, and have greater degrees of habitat complexity than other impounded lentic systems. Therefore, changes to the sport fish community at FNWR, after vegetation reduction, were anticipated to be similar to changes observed at Lake Marion.

Utilization of Grass Carp for Controlling Aquatic Vegetation

Grass carp were first utilized for control of aquatic vegetation in Arkansas in the mid 1960s. Originally introduced to Arkansas for control of aquatic vegetation in state hatchery ponds, grass carp were later stocked into other aquatic ecosystems (Kelly et. al 2011). The first stocking of grass carp in a wild fishery in Arkansas was at Lake

Greenlee in 1968 (Kelly et al. 2011; Bailey and Boyd 1971). Since then, grass carp have been stocked into more than 100 Arkansas lakes (Robinson and Buchanan 1988).

Grass carp have been extensively outside Arkansas for vegetation control. In 1976, a vegetation control project was initiated in Lake Conway in Orlando, Florida. Lake Conway is a 737-ha lake, composed of five interconnected pools consisting of Lake Gatlin, the east and west pools of Little Lake Conway, and the middle and south pools of Lake Conway proper. The objective of the Lake Conway study was to examine the ability of triploid and diploid grass carp to control hydrilla and to examine the collateral effects on the aquatic ecosystem (Leslie et al. 1994). The study found appreciable reduction in hydrilla with no discernible effect on other aquatic vegetation 2 years after stocking at a density of 10 grass carp/ha. Hydrilla biomass was reduced by 99% and maintained at low biomass for over 15 years, with negligible impact on other submerged aquatic vegetation species (Leslie et al. 1994).

A large-scale grass carp evaluation study was conducted in Lake Conroe, Texas in the early 1980s. Lake Conroe is an 8,100-ha highly developed reservoir. The reservoir was dominated by coontail *Ceratophyllum demersum*, hydrilla, and Eurasian watermilfoil *Myriophyllum spicatum* (Bettoli et al. 1992), with submerged vegetation covering 44% of the surface area (Martyn et al. 1986; Maceina et al. 1991). In 1981-1982, 33 grass carp/ha (Maceina et al. 1991) were stocked over a 12-month period. Within 2 years of stocking, total elimination of all aquatic vegetation occurred (Bettoli et al. 1992; Bettoli et al. 1993) with no appreciable re-growth having occurred by 1986 (Maceina et al. 1991).

Lake Marion, South Carolina, is a 10,000-ha reservoir on the Santee Cooper River system at the confluence of the Wateree and Congaree rivers (Kilgore et al. 1998). Grass carp were utilized to control submerged vegetation in 1989 (Morrow et al. 1997). The dominant vegetation was hydrilla, but egeria *Egeria densa*, coontail, slender naiad *Najas minor*, pondweed *Potamogeton* spp., and water primrose *Ludwigia* spp. were also present (Killgore et al. 1998). Grass carp were stocked at a rate of 17 fish/vegetated ha (Morrow et al. 1997). Vegetation coverage at stocking was ~ 5,000 ha (Kirk et al. 2000). By 1994, hydrilla coverage was reduced to approximately 60 ha (Killgore et al. 1998).

Bioenergetics Modeling of Grass Carp

The bioenergetics model is a balanced energy equation. Energy intake equals all energy outputs (Harvey 2005). The basic model equation is:

$$C = (R + A + S) + (F + U) + (DB + G),$$

C = consumption;
R = respiration;
A = active metabolism;
S = specific dynamic action (digestive costs);
F = egestion;
U = excretion;
DB = somatic growth;
G = gonad production.

Growth in biomass is linked to energy intake and losses (Railsback and Rose 1999). Thus, grams of biomass can be relatable to energy intake in joules (Wahl and Stein 1991).

Grass carp growth is related to metabolic energy demand and ingestion rates. Wiley and Wike (1986) reported high ingestion rates with low metabolic demand, offset by a low assimilation rate for grass carp under laboratory conditions. Their results indicated a high net energy gain that translated into high growth rates. The bioenergetic strategy of grass carp is to incur minimal metabolic costs while maximizing ingestion (Wiley and Wike 1986). However, consumption rates on an annual basis depend on fish size, population density, temperature, and food availability (Gasaway 1978; Shireman et al. 1980; Morrow et al. 1997). Growth in weight of grass carp was reported to be linearly related to age in the presence of abundant hydrilla (Gasaway 1978). Therefore, as grass carp get older and biomass increases, food consumption must increase to maintain linear growth.

Understanding grass carp bioenergetics is useful to assessing their impact on aquatic ecosystems. Bioenergetics models integrate food consumption, digestion, and absorption with growth rates (Hansen et al 1993). These models allow forecasting of the effects that grass carp have on aquatic vegetation. Masser (2002) reported grass carp effectiveness decreases after ages 5 to 7. Consumption as a percentage of body weight declines for grass carp as size increases. For example, smaller grass carp less than 3 kg consume 100% of their body weight per day. Grass carp weighing 3-6 kg consume 75% of body weight per day. Larger grass carp (> 6 kg) consume 26-28% of their body weight per day (Cassani 1996).

Understanding feed conversion rates of different sizes of grass carp is essential to predicting growth among cohorts. Sutton (1974) reported that for a 1 g increase in grass carp growth of a 176-g fish, required 5 g of dry hydrilla. Growth in large fish (753 g) fluctuated over a period of 2 weeks, though the amount of hydrilla consumed remained constant. Small grass carp (176 g) were more efficient at converting hydrilla to fish flesh than large grass carp. Growth rates were similar between the two sizes of grass carp, but large fish consumed 50% more hydrilla (in terms of biomass) than small fish (Sutton 1974). Michewicz et al. (1972) reported an increase of 10 g in fish flesh corresponded to a consumption of 2,800 g of lettuce *Lactua* spp. fresh weight or 133 g of lettuce dry weight in 760-g fish (Stott and Orr 1970). Understanding these consumption-growth relationships enables lake managers to forecast how many fish are needed effectively control vegetation outbreaks.

The types of vegetation consumed by grass carp are dependent on temperature (Chapman and Coffee 1971), fish age and size (Shireman and Maceina 1980), and plant species (Shireman et al. 1978). Grass carp will consume many species of algae and aquatic plants, depending on availability within the aquatic environment (Fedorenko and Fraser 1978). However, grass carp assimilation rates may play a role in selection of vegetation for consumption. The effect of temperature upon feeding indicates feeding rate increases to an optimum and decreases beyond this optimum (Kitchell et al. 1974). Consumption and respiration control growth rates while temperature and fish size are key variables when determining the rates of consumption and respiration. Weight gain and losses are modeled as a function of temperature and consumption (Kitchell et al. 1977). Therefore, bioenergetics modeling may allow the user to elucidate the processes controlling growth, relating growth to food consumption, temperature, and fish size. Thus, allowing lake managers a better understanding when to plan periodic re-stockings of grass carp to maintain effective vegetation control.

Methods

Study Area

The study area for this research was FNWR. The U.S. Fish and Wildlife Service (USFWS) established Felsenthal National Wildlife Refuge in southeast Arkansas in 1975. Felsenthal National Wildlife Refuge is approximately 12 km west of the town of Crossett, and 48 km east of El Dorado. Felsenthal National Wildlife Refuge is a 26,304-ha wildlife refuge (Figure 1) containing an abundance of aquatic resources. The Ouachita and Saline rivers and the Felsenthal Reservoir comprise most of the refuge. The 4,074-ha Felsenthal Reservoir lies on the Ouachita River and was formed by the Felsenthal Lock and Dam. The Felsenthal Reservoir is primarily the backwater areas of the Ouachita River system. Felsenthal Reservoir is bisected by creeks, sloughs, buttonbush swamps, and lakes, and bisected by the Ouachita River (Olive et al. 2010). Felsenthal National Wildlife Refuge has experienced nuisance aquatic vegetation issues over the past 20 years, and was the site of the grass carp telemetry study (Olive et al. 2010).

Before this study could assess aquatic vegetation in FNWR, Arkansas Game and Fish Commission applied a 1% glyphosate herbicide to emergent aquatic vegetation in three locations on the east and west part. To assess the effectiveness of the herbicide application three transects were randomly chosen in each of the three locations. The outer edge of the emergent vegetation was visually determined, and a GPS waypoint was generated representing the pelagic edge of the emergent vegetation. Using a 3-m Jon boat, one person maneuvered through the emergent vegetation to the shoreline, where a second GPS waypoint was generated. The width of emergent vegetation (i.e., the distance between GPS waypoints) was measured using Bushnell Yardage Pro laser range finder binoculars (Bushnell, Overland Park, Kansas). Percent coverage along each transect was visually estimated. Ten weeks after the herbicide application, estimates of emergent vegetation width and percent coverage were repeated.

Aquatic Vegetation Coverage and Biomass

For this study, FNWR was divided into three parts – designated north, east, and west. The north part consisted of all areas in the refuge north of U.S. Highway 82. The east and west parts were south of Highway 82, and were separated by the main channel of the Ouachita River. Twenty-one unique locations, distributed among the three parts of the refuge, were sampled to estimate the coverage and biomass of submerged and emerged aquatic vegetation. Don Thurman, an AGFC district biologist, added two locations (Red-eye and Pete Wilson) in the east part, thus, increasing vegetation sampling to twenty-three locations.

Within each location, three transects (two littoral and one pelagic) were randomly selected by superimposing a handmade grid with numbered quadrats over a map of the refuge. Each grid quadrat was 1,600 m^2 in area, and was further sub-divided into four 400-m^2 quarter quadrats. Three quadrats were chosen from each location using a random number generator. Then, one of the quarter quadrats was randomly selected within each quadrat also randomly selected using a random number generator. Global Positioning System waypoints representing the midpoint of the upstream most quarter quadrat boundary were recorded, representing a transect starting point. Each transect spanned 20 m and ran parallel to the littoral edge of the water body. Where shoreline was unidentifiable, the transect ran in the direction of flow. Compass direction of all transects were recorded. A 4-m stake with a rope attached was driven into the sediment at each GPS starting points. In an arcing fashion, a boat traveled to the end of the 20-m transect where another stake was driven into the sediment. The boat then traveled the length of the 20-m transect 0.2 m from the transect line. The aquatic vegetation overlaid by the rope was visually estimated and recorded at 0.5-m intervals.

On each of the 69 transects a 1-m^2 quadrat was sampled to obtain vegetation biomass estimates (Bonar et al. 1993). A 1-m^2 quadrat sampler, constructed from polyvinylchloride pipe and polypropylene netting was placed adjacent to the line transect, 10 m from the starting point of the transect. The sampler was lowered into the water until it rested on the bottom. The floating vegetation was skimmed off using a dip net and placed in a plastic bag labeled with the location, date, and quadrat number. Submerged vegetation was severed from the bottom using an Aquatic Weed Eradicator© (Northern Tool and Equipment, Burnsville, Minnesota), netted and using a long-handled net and placed in a mesh onion sac. When all vegetation was removed from the quadrat (i.e., no additional vegetation netted on three consecutive attempts), the samples were labeled with the location, date, and quadrat number.

Processing of vegetation from each of the quadrat samples included rinsing the vegetation while it was still in the onion sac, spinning the sample in a washing machine for 1 min, separating the vegetation into species, and weighing each vegetation species on a spring scale to the nearest gram (i.e., spun wet weight; Bonar et al. 1993). Vegetation sampling was performed in the fall 2008 and fall 2010. Record flooding during fall 2009 prohibited vegetation sampling in that year.

Exclusion Cages

In April 2010, ten exclusion cages were installed in FNWR. Exclusion cages were distributed equally between the east and the west parts of the refuge. No exclusion cages were constructed in the north part due to limited submerged vegetation in the 2008 vegetation assessment. Five locations in each of the two parts were randomly selected from a list of all locations within a part. Exclusion cage sites within each location were determined following the same protocol as vegetation transects (Table 1). Exclusion cages consisted of four 3.7-m metal signposts driven into the substrate approximately 2 m apart in a square pattern forming a 4-m^2 area. Black polypropylene netting, (Industrial Netting, Minneapolis, Minnesota) was formed into a 4-m^2 cylinder using zip ties. A 10-mm diameter lead chain was attached to the bottom of each cylinder using zip ties. The cylinder was then placed over the signposts lowered to the substrate and zip tied to two of the signposts. Signs indicating a "closed area" were attached to the signposts in the direction of boat travel to alert boaters of the exclusion cage area and to request that the exclusion cages be left undisturbed. Exclusion cages were sampled in December of 2010. Vegetation sampling was performed as previously described.

Modeling Grass Carp Consumption Using Conversion Ratios from Literature

Grass carp growth estimates were related to aquatic vegetation consumption using two reported conversion ratios (Mitzner 1978; Venkatesh and Shetty 1978). In April 2009, 50 grass carp were weighed to the nearest gram before being stocked into FNWR. These data provided a range of grass carp weights at stocking. Subsequently, two grass carp were collected during electrofishing for sportfish population assessments, and William Pippen, a commercial angler, collected eight grass carp in gill and hoop nets. Each of these grass carp were weighed to the nearest gram, providing a range of grass carp weights approximately one year after stocking. Differences between initial and final weights of grass carp provided a range of annual observed weight gains. Venkatesh and Shetty (1978) observed that consumption of 94 g of hydrilla and coontail were required for every gram of fish growth. Mitzner (1978) reported that consumption of 48 g of napier grass *Pennisetum purpureum* was required for 1 g of fish growth. I also considered the effect of a median conversion ratio of 71 g vegetation/g fish flesh. The conversion ratios and estimates of annual observed weight gain were used to estimate a range of values for annual individual consumption.

The number of grass carp stocked in the refuge, estimates of annual individual consumption, and estimates of annual mortality from the literature were used to generate a range of annual population consumption estimates. Literature estimates of total annual mortality for stocked grass carp ranged from 1% (Shireman et al. 1980) - 33% (Mitzner 1978; Hill 1986), and from these estimates, I considered the median total annual mortality rate of 17%. Each month, the size of the grass carp population was diminished by $1/12^{th}$ the total annual mortality. Each month, individuals in the population were assumed to gain $1/12^{th}$ the annual weight gain. The monthly population consumption was the number of individuals alive at the end of the month times the monthly weight gain times the conversion ratio. The annual population consumption was the sum of the monthly population consumptions. The annual population consumption was standardized by refuge area to determine area specific consumption rate as $g \cdot m^{-2} \cdot year^{-1}$.

The area specific consumption was divided by the area specific hydrilla production to generate a ratio of consumption to production (C:P ratio). This ratio was used to approximate the ability of grass carp to control hydrilla production in the refuge. Estimates of area specific hydrilla production were taken from biomass measurements in grass carp exclusion cages approximately one year after cages were installed. Combinations of variables (lowest initial weight, highest final weight, highest conversion ratio, lowest annual mortality, and lowest area specific hydrilla production) were used to generate the maximum possible C:P ratio. Likewise, combinations of variables (highest initial weight, lowest final weight, lowest conversion ratio, highest annual mortality, and highest area specific hydrilla production) were used to generate the minimum possible C:P ratio. Median values for the same set of variables were used to generate a median estimate of the C:P ratio.

Bioenergetics Modeling of Consumption by Grass Carp

Estimates of annual individual consumption were generated using Wisconsin Bioenergetics 3.0 (Hanson et al. 1997) to model consumption in relation to observed weight gain and temperature. Parameters of growth were based on data generated during this study, while other grass carp-specific parameters were taken from literature. Parameters were taken from a model of tilapia *Sarotheradon spp*. bioenergetics (Nitithamyong 1988), because tilapia was the only non-piscivorous species for which certain parameters were available. Consumption was modeled using a 365-d simulation, with initial and final observed weights of grass carp from this study were used to determine annual observed weight gain. The initial population was set at one with 0%

annual mortality so individual annual consumption could be estimated. Consumption model 1 and respiration model 1 from Wisconsin Bioenergetics 3.0 were used in this exercise. We ran the model with no spawning and no chance of mortality for the individual. Maintenance temperature was set at 17.1^{o}Caccording to Wiley and Wike (1986).

User input data were manually entered into the model. Diet proportion was set at 100% hydrilla during the entire 365-d simulation (Table 2). Prey energy density and predator energy density were set at 1,330 J/g wet weight (Cummins and Wuycheck 1971; Table 2) and 5,639 J/g wet weight (Reagan 1969), respectively. Both energy densities were fixed throughout the 365-d simulation. Site-specific temperature data were recorded using a Pendant temperature/light data logger, (MicroDAQ, Contoocook, New Hampshire). Temperature data were recorded at 4-h intervals and averaged on a daily basis.

Consumption parameters were entered as grass carp specific values from literature whenever possible. This exercise used consumption equation 2, the temperature-dependent equation for consumption by warmwater species (Kitchell et al. 1977; Table 2). Consumption parameters Ca and Cb were taken from Kilambi and Robison (1979). Consumption parameters Ck1, Ck4, Cq, Ctl, Ctm, and ration were default settings for tilapia. Critical temperature optimum (Cto) was 23.8^{o}C, which was the median temperature of the range cited in Kilambi and Robison (1979).

Egestion and excretion were modeled using equation set 1 (Kitchell et al. 1977), which computed these variables as a constant proportion of consumption. Egestion (Fa) was varied from 0.36 (default setting for tilapia) to 0.60 at increments of 0.04 (Table 2).

Cui et al. (1994) indicated that grass carp egest approximately 52% of what they consume. The variable Ua was set according to Carter and Brafield (1992a). As mentioned above, predator caloric density did not vary with body mass.

Respiration was modeled using equation 2, which adjusts respiration for fish size, temperature, and activity level (Kitchell et al. 1977). Activity (Act) was varied between levels of 2 and 3 because we were uncertain of the amount of grass carp activity (Table 2). Parameters to calculate gram specific oxygen consumption, Ra and Rb, were set at 0.17 and -0.35, respectively, according to Carter and Brafield (1992b). Respiration parameters Rq, Rtm, Rto, and Sda were set at default settings for tilapia.

Weight gain was set at the maximum, median, and minimum observed values from our study. Consumption was initially modeled setting Act, Fa, and Cto at median values of 2.5, 0.48, and 23.8, respectively. The model run using the median observed weight gain represented the base case, or best possible estimate of annual individual consumption, based on a bioenergetic modeling approach. A simple sensitivity analysis was then performed by varying four uncertain user input parameters, Act, Fa, Cto, and weight gain. One of the uncertain values was varied, while the other user input parameters were held constant at their median values. Weight gain was modeled at ± 25% of the median weight gain. Activity was modeled at ± 25% of the median of 2.5. Egestion was modeled at ± 25% around the median of 0.48. The Cto was modeled at ± 24% around the median of 23.8°C. The percent difference in annual individual consumption, relative to the base case, was calculated as each of the uncertain user input parameters was singularly varied. This approach was expected to add robustness to model predictions and interpretation of uncertain parameters effect on the model.

In summary, the Wisconsin Bioenergetics 3.0 was used to predict total daily consumption per individual as a function of weight gain and temperature. Total daily consumption was summed over the 365-d simulation to generate annual individual consumption. Annual individual consumptions from the bioenergetics modeling exercise were compared to estimates generated by modeling annual individual consumption using conversion ratios from literature. In addition, we modeled annual individual consumption varying Act, Fa, Cto, and weight gain singularly in a simple sensitivity analysis.

Fish Population Characteristics and Catch per Unit Effort

Sportfish populations were assessed in 2008, before grass carp stocking, and in 2009 and 2010 after grass carp stocking. Approximately 300 bluegill and 300 largemouth bass were collected each year for analyses of catch per unit effort, age and growth, size structure, and mortality. All collections were made using a Smith-Root (Vancouver, Washington) GPP 7.5 boat mounted electrofisher set at 500-V DC current and 60 Hz.

A minimum of 100 largemouth bass and 100 bluegill were sampled from each of the three parts of the refuge in each of the 3 years of sampling. Fishes were collected from seven randomly selected locations from each refuge part during each year. Coordinates for the starting points of two transects per location were randomly selected, as before, for vegetation transects. Each transect consisted of a 10-min electrofishing run, parallel to the shoreline. Fish were placed in a bag labeled with the location, date, starting GPS coordinates, and number of specimens of each species. Bags were frozen until further processing could occur. In the lab, all fish were weighed to the nearest gram and measured for TL to the nearest millimeter. Sagittal otoliths were removed, wiped clean of blood and mucous, patted dry, and placed in a scale envelope marked with the date, location, transect, species, and fish ID.

Catch per unit effort (CPUE) and descriptive statistics were calculated for both species in each year of the study. Proportional size distribution of quality size fish (PSD), and proportional size distribution of preferred size fish (PSD-P) were calculated to assess size structure of sportfish populations (Willis et al. 1993; Guy et al 2007). Relative weight (W_r) measures were used to assess fish condition (Wege and Anderson 1978).

Sagittal otoliths were utilized for age analysis. Two readers independently estimated the age of each fish from whole otoliths without knowledge of the length, weight, or gender of the fish. When a disagreement occurred between the two readers, a third reader estimated age of the fish. After consultation among all three readers, an agreed upon age was assigned to the fish in dispute. Growth was examined by calculating the parameters of the von Bertalanffy equation (Guy and Brown 2007). Age frequency distributions were used to estimate total annual mortality for both sportfish populations during each year of the study.

Statistical Analysis

All statistical analyses were performed using SAS 9.2® (SAS Institute, Cary, North Carolina 2008). Vegetation percent coverage was quantified using a standard percent scale (0-100%). Percent coverage for each location was the average of the percent coverage from the three transects at each location. Likewise, biomass for each location was the average of the biomass from the three quadrats at each location. Hence, locations (n=21) were considered the experimental unit. Percent coverage and biomass data were rank transformed before statistical analyses. Repeated measures analyses (PROC MIXED) were used to examine the effect of year (i.e., 2008 was before and 2010 was after grass carp stocking) and refuge part on percent coverage, total vegetation biomass, hydrilla biomass, and American lotus biomass. A nonparametric one-way ANOVA (PROC NPAR1WAY) with a post hoc Wilcoxon test was also used to compare differences in mean percent coverage and biomass. To examine similarities between vegetation communities in 2008 and 2010, two percent similarity indices were calculated one using percent coverage data and another with biomass data. Total vegetation biomass, hydrilla biomass, and American lotus biomass inside and outside of the exclusion cages were compared using paired T-tests (PROC TTEST).

Estimates of CPUE and several population characteristics for bluegill and largemouth bass were computed separately and compared statistically. Mean CPUE for an individual location was the average CPUE from the three electrofishing transects at each location. All fish from the three electrofishing transects from a location were combined into one sample to calculate a population characteristic for the location. In most analyses, location was the experimental unit. Repeated measures analyses (PROC MIXED) were used to assess differences in sportfish population characteristics among the three parts of the refuge and over time. A least significant difference (LSD) test was used to compare differences among means from the refuge parts, and the 2 years of the study. One exception to this procedure was the examination of growth. For this analysis, all fish caught in a given year were combined into one sample and used to generate composite von Bertalanffy parameters for that year. In this case, years were the experimental units. Comparison of composite von Bertalanffy parameters were done by examining the degree of overlap using 95% CI's for each parameter. Another exception to this procedure was the examination of total annual mortality. For this measure, all fish from a refuge part were combined into a single composite sample, and used to generate a single catch curve for each refuge part during each year of the study. In this case, the parts were the experimental units. Differences in mean total annual mortality were examined using a one-way ANOVA.

Results

Preliminary Emergent Vegetation Coverage

Mean width of emergent vegetation initially ranged from 44.7 - 127.3 m (Table 3). Mean percent coverage initially ranged from 64.3 - 83.3%. Emergent vegetation was influenced by the herbicide application in August 2008 and may have also been affected by extended periods of high water that occurred in September 2008 (Figure 2). At all three locations, emergent vegetation was completely eliminated on all transects (Table 3).

Aquatic Vegetation Percent Coverage and Biomass

Aquatic vegetation percent coverage was estimated in 2008 and 2010. Mean (SD) percent coverage was 11.5% (28.7) and 33.3% (45.8) in 2008 and 2010, respectively (Table 4). There was a difference in percent coverage among parts (F = 7.47, df = 20, P < 0.004). Percent coverage in the east and west parts were 23.8% (12.7) and 31.1% (12.4), respectively, while the percent coverage in the north part was only 15.5% (6.9). The year effect and the interaction were not significant. However, the Wilcoxon rank sums test indicated percent coverage was significantly different between years (P = 0.049).

Aquatic vegetation biomass was estimated in 2008 and 2010. Mean biomass was 57.8 (157.2) g/m^2 138.1 (346.5) g/m^2 in 2008 and 2010, respectively (Table 4). There was a difference in biomass among parts (F = 3.72, df = 20, P = 0.042). Biomass in the east and west parts were 24.5 (13.1) g/m^2 and 30.6 (11.1) g/m^2, respectively, while biomass in the north was 15.1 (11.3) g/m^2. The year effect and the interaction were not significant. The Wilcoxon rank sums test indicated biomass was not significantly different between years. The interaction was significant in the analysis of mean hydrilla biomass (F = 4.04, df = 20, P = 0.034). The source of the interaction appears to be the result of an inconsistent response among parts over time. In the east and parts mean hydrilla biomass decreased, while mean hydrilla biomass in the north part appeared stable. There were no significant differences in the repeated measures ANOVA for American lotus biomass.

Dominant vegetation in each year was compared. The vegetation community before grass carp stocking, based on biomass, was dominated by American lotus, hydrilla, egeria, coontail, and duckweed (Table 5). The vegetation community after grass carp stocking, based on biomass, was dominated by American lotus, fragrant water lily *Nymphaea odorata*, coontail, duckweed, and hydrilla.

Relative abundances of individual species of vegetation were estimated in 2008 and 2010. In 2008, American lotus and hydrilla together comprised 76.8% of the vegetation biomass (Table 6). In 2010, American lotus comprised 81.0% and hydrilla was less than 1% of the vegetation biomass. Coontail and egeria comprised 9.4% and 11.0% of the vegetation biomass in 2008, respectively. By 2010, these two species each comprised less than 1% of the vegetation biomass (Table 6). Conversely, fragrant water lily comprised less than 1% of the vegetation biomass in 2008, but comprised 18.3% of the biomass in 2010. Submerged vegetation comprised 56.2% of the 2008 vegetation biomass, while floating and emergent vegetation comprised the remaining 43.8%. However, by 2010, 99.4% of the vegetation biomass was floating or emergent (Table 7). The percent similarity index indicated a 57.7% similarity in vegetation communities between years based on percent coverage data (Table 8). Percent similarity based on biomass data indicated only a 41.7% similarity in vegetation communities between years.

Exclusion Cage Vegetation Estimates and Biomass Comparisons

Vegetation samples from inside and outside of grass carp exclusion cages were collected in the fall of 2010, approximately one growing season after placement of exclusion cages. Seven of the ten locations were found to contain aquatic vegetation either inside or outside of the exclusion cage (Table 9). Six of the inside samples contained hydrilla, whereas only three of the outside samples contained hydrilla. Biomass of hydrilla ranged from 0 – 2,275 g in inside samples and 0 – 3 g in outside samples. Hydrilla biomass differed significantly between the inside and outside samples of the exclusion cages ($T = 2.18$, df = 18, $P = 0.043$). Mean hydrilla biomass was almost 500 times greater in samples from inside exclusion cages. Four inside samples and three outside samples contained American lotus. Biomass of American lotus from inside and outside samples ranged from 0 – 1,854 g and 0 – 437 g, respectively. American lotus biomass did not differ significantly between inside and outside samples of the exclusion cages ($T = 0.98$, df = 18, $P = 0.342$). Total vegetation biomass differed significantly between samples inside and outside the exclusion cages ($T = 2.43$, df = 18, $P = 0.026$). Total vegetation was greater inside the exclusion cages compared to that observed outside the exclusion cages.

Modeling Grass Carp Consumption as a Proportion of Production

Annual individual consumption and annual population consumption of grass carp in FNWR were calculated using observed weight gains, literature values for feed conversion, and literature values for total annual mortality. The maximum, median, and minimum observed grass carp weight gains were 3,029, 1,766, and 1,047 g, respectively (Table 10). Model estimates for the maximum, median, and minimum annual individual consumption by grass carp were 284,726, 125,386, and 50,256 g vegetation/year, respectively (Table 11). Considering the number of fish stocked and total annual mortality, annual population consumption ranged from 2.79×10^{9} - 1.92×10^{10} g vegetation/year. Area specific population consumption rates ranged from 56 - 474 $g \cdot m^{-2} \cdot year^{-1}$. Area specific hydrilla production estimates, based on hydrilla biomass in grass carp exclusion cages after one growing season, ranged from 0 - 2,276 $g \cdot m^{-2} \cdot year^{-1}$ (Table 9). It is not possible to calculate a C:P ratio when production was zero, so the lowest non-zero estimate of hydrilla production was used to calculate the maximum C:P ratio (Table 10). Zeros were considered when determining the median area specific production for hydrilla. Using this approach, calculated C:P ratios ranged from 0.03 - 73.99 (Table 10). Hence, grass carp consumption ranged from 3 - 7,399% of hydrilla production. The median values for all parameters considered suggested that grass carp consumption was 1,190% of hydrilla production.

Bioenergetics Modeling of Consumption by Grass Carp

Grass carp annual individual consumption was modeled using the Wisconsin Bioenergetics Model. As above, the maximum, median, and minimum weight gains used were 3,029, 1,766, and 1,047 g, respectively. The annual individual consumptions were 150,990, 148,650, and 151,912 g vegetation/year for the maximum, median, and minimum weight gains, respectively (Table 11). Annual individual consumption estimates were compared between modeling methods at maximum, median, and minimum observed weight gains. The conversion ratio method produced the highest and lowest annual individual consumption estimates (Table 11). Hence, all estimates of annual individual consumption using the bioenergetic method were within the range of values produced by the conversion ratio method.

The sensitivity analyses varied Act, Fa, Cto, and observed weight gain individually, and compared the predicted annual individual consumption to the annual individual consumption from the base case. When Act was modeled at ± 25% of the median value of 2.5, annual individual consumption was 119,135 and 179,657 g vegetation/year (Table 12). Annual individual consumption changed by -19.9% and 20.9%. When Fa was modeled at ± 25% of the median value of 0.48, annual individual consumption was 120,779 and 193,249 g vegetation/year. Annual individual consumption changed by -18.8% and 30.0%. When Cto was modeled at ± 24% of the median value of 23.8ºC, annual individual consumption was 260,394 and 92,975 g vegetation/year. Annual individual consumption changed by 75.2% and -37.5%. When weight gain was modeled at ± 25% of the median value of 1,766 g, annual individual consumption was 130,356 and 154,188 g vegetation/year, which corresponded to changes in annual individual consumption of -12.3% and 3.7%, respectively.

Catch per Unit Effort and Fish Population Characteristics Comparisons

Bluegill.--Bluegill catch per unit effort (CPUE) and population characteristics were compared among refuge parts and between years. The interaction was significant in the repeated measures ANOVA (F = 3.70, df = 35, P = 0.013). The source of the interaction appears to be the result of an inconsistent response among refuge parts over time. Mean CPUE in the east and west were consistent through time, but mean CPUE in the north was much higher in 2009 than 2008 or 2010 (Figure 5).

Proportional size distribution was moderate throughout the study. The interaction term was significant in the repeated measures ANOVA (F = 7.14, df = 35, P < 0.001). The source of the interaction appears to be the result of an inconsistent response among refuge parts over time. Mean PSD increased notably in the north part, but decreased slightly in the east part. The trend was mixed in the west part (Figure 6).

Proportional size distribution of preferred size fish varied during the study. There was a difference in PSD-P between parts (F = 8.63, df = 18, P < 0.002). The year and the interaction between year and part were not significant. Mean PSD-P in the east part was greater than mean PSD-P in the north and west parts (Figure 7).

Relative weight varied among years and among parts. The interaction was significant in the repeated measures ANOVA (F = 3.81, df = 36, P = 0.011). The source of the interaction appears to be the result of an inconsistent response among refuge parts over time. There was a consistent decline in mean W_r in the east part, but the trends were mixed in the north and west parts (Figure 8). During 2010, mean W_r was low for all parts of the refuge.

Mean total length at age 1 ranged from 88.8 - 199.9 mm during the study. The interaction was significant in the repeated measures ANOVA (F = 20.08, df = 27, P < 0.001). Mean length at age 1 in the east and west part remained relatively constant during the study (Figure 9). However, mean length at age 1 increased in the north part. Total annual mortality of bluegill was calculated separately for each of the three parts, during each year of the study. Mean total annual mortality ranged from 54 - 87% (Figure 10). Mean total annual mortality was significantly higher in 2009 than in 2008 or 2010 (F = 11.73, df = 5, P = 0.009).

Von Bertalanffy growth parameters were calculated on a yearly basis. Estimates of L-infinity (L_∞), growth rate (k), and t_0 ranged from 234.9 - 430.9 mm, 0.107 - 0.375, and -1.46 - -1.91, respectively (Table 13). Despite some variability among years, degree of overlap of 95% confidence limits suggested none of the three parameters differed significantly among years during the study.

Largemouth bass.--Largemouth bass population characteristics were also compared among years and among refuge parts. Catch per unit effort ranged from 10.3 - 36.6 fish/h. The part effect and the interaction were not significant. However, there was a difference in mean CPUE among years (F = 18.14, df = 35, P < 0.001). Mean CPUE in 2008 was significantly lower than mean CPUE in 2009 and 2010 (Figure 11).

Proportional size distribution of quality size fish varied throughout the study. Mean PSD ranged from 25.5 - 66.0. As above, the part effect and the interaction term were not significant, but the year effect was significant (F = 4.74, df = 29, P = 0.016). Mean PSD was significantly higher in 2008 than in 2009 or 2010 (Figure 12), with no differences detected between 2009 and 2010.

Proportional size distribution of preferred size fish varied much the same as largemouth bass PSD of quality size fish. Mean PSD-P ranged from 0.0 - 33.2. There was a significant year effect (F = 4.04, df = 29, P = 0.028), but the part effect and the interaction were not significant. As with PSD, mean PSD-P was significantly higher in 2008 than 2009 or 2010 (Figure 13).

Mean W_r ranged from 95.4 - 109.6 over the years of the study. There was a significant year effect (F = 5.45, df = 36, P = 0.009), but part and the interaction were not significant. Unlike previous population characteristic results, mean W_r in 2008 and 2009 were not significantly different, but both values were greater than mean W_r in 2010 (Figure 14).

Mean total length at age 1 for largemouth bass ranged from 172.5 - 277.3 mm during the study. The interaction was significant in the repeated measures ANOVA (F = 5.65, df = 20, P = 0.006). The source of the interaction appears to be the result of an inconsistent response among refuge parts over time. Mean length at age 1 in the east and west part remained relatively constant during the study (Figure 15). However, mean length at age-1 increased in the north part. No age-1 fish were sampled in the north part in 2009.

Mean total annual mortality for largemouth bass was calculated using part as the experimental unit. Mean total annual mortality ranged from 63 - 81% during the study. Mean total annual mortality was not significantly different among the years (Figure 16).

Growth parameters from the von Bertalanffy equation were calculated for each year. Estimates of L_∞, k, and t_0 ranged from 475.0 - 966.4 mm, 0.114 - 0.543, and -1.18 - 0.55, respectively (Table 14). As with bluegill, the L_∞ value for largemouth bass in 2010 was 450 mm larger than the L_∞ values for 2008 and 2009. However, degree of overlap of 95% confidence limit suggested none of the von Bertalanffy values differed significantly among years.

Discussion

Vegetation Changes

The virtual elimination of submerged vegetation, as observed during this study in FNWR, was also reported in other large-scale grass carp vegetation control studies. In Lake Conroe, Texas, Maceina et al. (1991) reported elimination of all submerged vegetation after grass carp stocking. Control of submerged vegetation in Guntersville Reservoir, Alabama using grass carp resulted in a 36% decline in all submerged vegetation species, and near elimination of hydrilla (Webb et al. 1994). Introducing grass carp to control hydrilla in Lake Marion, South Carolina resulted in elimination of hydrilla and most other submerged vegetation (Kirk and Henderson 2006).

Grass carp do not appear to discriminate between native and nonnative submerged vegetation, and will readily control both types. In general, grass carp appear to control both native and nonnative submerged vegetation. The dominant submerged vegetation before grass carp stocking in FNWR included native and nonnative species (hydrilla, egeria, and coontail). Native and nonnative submerged vegetation were also controlled in other reports on reservoirs. Dominant submerged vegetation in Lake Conroe, at the time of grass carp stocking, was hydrilla, Eurasian watermilfoil, and coontail (Martyn et al. 1986). Exotic submerged vegetation in Guntersville Reservoir prior to grass carp stocking included Eurasian watermilfoil, spinyleaf naiad *Najas marina*, and hydrilla. However, native species such as southern naiad *Najas guadalupensis*, coontail, American pondweed *Potamogeton nodosus*, small pondweed *Potamogeton pusillus*, and muskgrass *Chara zeylandica* were also creating problems in Guntersville reservoir (Webb et al.

1994; Wrenn et al. 1994). In Lake Marion, the dominant submerged vegetation was hydrilla and egeria (Killgore and Kirk 1998; Kirk and Henderson 2006). Grass carp do not appear to discriminate between native and nonnative submerged vegetation.

Control of submerged vegetation with grass carp appears to occur quickly. Submerged vegetation in FNWR was drastically reduced just 2 years after grass carp stocking. In Lake Conroe, submerged vegetation was eliminated 2 years after grass carp stocking, with no appreciable regrowth observed four years after stocking (Maceina et al. 1991; Martyn et al. 1986). In Guntersville Reservoir, hydrilla and naiad spp. were reduced to less than one ha, 1 year after grass carp stocking with no appreciable re-growth (Webb et al. 1994).

An obvious decline in hydrilla biomass was observed during this study after stocking grass carp. Furthermore, the difference in hydrilla biomass inside and outside of the exclusion cages supports the assertion that hydrilla reductions were largely attributable to grass carp consumption as opposed to other environmental factors. Consumption estimates using bioenergetics modeling indicated the number of grass carp stocked could have easily consumed all the hydrilla in FNWR. Despite the uncertainties associated with mortality and conversion ratios from the literature, and parameters in the bioenergetics model, grass carp consumption could have accounted for more than 11 times the median observed hydrilla production. It is important to note that the large variation in the range of production to consumption ratios was due to calculation of this ratio at maximum, median, and minimum values of weight gain and hydrilla production. Nevertheless, both methods of calculating grass carp consumption indicate that grass carp could control the amount of hydrilla production observed in FNWR.

The elimination of virtually all submerged vegetation in FNWR led to a major shift in the aquatic vegetation community. The FNWR shifted from a system dominated by submerged vegetation to a system dominated by emergent and floating vegetation. This type of shift in vegetation communities was not reported in other studies. Surveys of the aquatic plant community in Lake Conroe before vegetation control identified 18 species of aquatic plants (Matryn et al. 1986). Although Klussman et al. (1988) reported water hyacinth *Eichornia crassipes* covered 200 ha in the northern end of Lake Conroe, no emergent vegetation species were surveyed before or after grass carp stocking. Maceina et al. (1991) reported emergent vegetation was scarce throughout Lake Conroe two years before, and three years after grass carp stocking. Other large-scale vegetation control projects failed to mention emergent or floating vegetation species when documenting aquatic vegetation communities at the time of grass carp stocking. This may be because most projects were focused on controlling exotic submerged vegetation, such as hydrilla and watermilfoil. Our holistic approach to assessing the vegetation community provides lake managers with better understanding of how vegetation control can have unintended consequences in a complex ecosystem.

Changes in Sportfish Populations

Increases in CPUE of selected sportfishes concurrent with control of submerged vegetation were observed in this and several other studies. Bluegill and largemouth CPUE in FNWR exhibited moderate increases during the study. Killgore and Kirk (1998) reported a significant increase in mean catch of bluegill and largemouth bass after hydrilla reduction in Lake Marion. Killgore et al. (1989) indicated a significant increase in total catch of largemouth bass and bluegill during low hydrilla coverage. Wrenn et al. (1994) reported significant increases in the CPUE of age-0 and age-1 largemouth bass 3 years after stocking grass carp in Guntersville Reservoir. However, some other studies have reported declines, or no changes, in sportfish CPUE after control of submerged vegetation. Webb et al. (1994) reported decreased CPUEs for largemouth bass in Lake Conroe after near elimination of submerged vegetation. Bettoli et al. (1993) reported a decline in largemouth bass and bluegill density in Lake Conroe after near elimination of submerged vegetation. In Arkansas and Florida, Bailey (1978) and Shireman et al. (1985) respectively, indicated no changes in sportfish abundances with decline in vegetation in two different large impoundments. It is conceivable that reductions in submerged vegetation influenced catchability of sportfish during electrofishing in our study. Increases in CPUE could have been, in part, an artifact of sampling un-vegetated littoral habitats. However, high water levels in 2008 and 2009 are believed to have resulted in strong year classes of bluegill and largemouth bass. The increases in CPUE were, in part, believed to be a function of those consecutive strong year classes.

The significant declines in sportfish W_r after reduction of submerged vegetation from this study were not observed during other vegetation control projects. Largemouth bass and bluegill W_r varied in FNWR throughout our study. However, mean W_r for both species were lowest in 2010. Mallison et al. (1994) reported increased W_r when submerged vegetation percent coverage was low (20%) in Lake Yale, Florida. Largemouth bass W_r increased slightly from 86 to 89 during their study (Mallison et al. 1994). Colle and Shireman (1980) reported repetitive temporal cycles of coefficients of condition for bluegill and largemouth bass. Annual trends in coefficients of condition were characterized by winter/spring increases and summer declines after grass carp stocking in Lakes Baldwin and Wales, Florida. However, no long-term trends in bluegill or largemouth bass coefficients of condition were evident (Colle and Shireman 1980). Bailey (1978) indicated improvement of largemouth bass and bluegill condition after reductions in submerged vegetation in 31 Arkansas lakes.

A reduction in submerged vegetation during this study likely resulted in increased predator-prey interactions. Largemouth bass, a visual predator, probably had greater feeding success after vegetation reduction, thus, increasing W_r in 2009. Bluegill W_r could have conceivably increased at the same time, because of a decline in competition among bluegill for food resources. The subsequent declines in W_r in 2010 may have been a lagged response due to an increase in density-dependent competition for food due to the two strong year classes of sportfishes. Experimental research needed to confirm this observation was beyond the scope of this study. Although significant changes in sportfish growth rates were not observed after the reduction of submerged vegetation in this study, growth rate changes were observed in other vegetation control projects. Cope et al. (1969; 1970) reported bluegill growth increased after submerged vegetation control. Pothoven et al. (1999) reported higher bluegill growth rates after chemical application to control aquatic vegetation. Pothoven (1999) further suggested that higher growth rates were due to reduced competition, due to the reduction of smaller fishes (Mittelbach 1981; Mittelbach and Osenberg 1993), or increased feeding efficiency in the absence of dense vegetation (Crowder and Cooper 1982). The same factors that led to the changes in sportfish W_r may have influenced changes in growth. We suspect that the changes in predator-prey interactions and density dependent competition that likely influenced W_r

also influenced growth, though not to the same magnitude, since no significant changes in growth were observed.

Size structure of sportfish populations was variable following control of submerged vegetation. Bluegill PSD and PSD-P varied throughout the study, with no clear trends through time in any of the refuge parts. Largemouth bass mean PSD and PSD-P were higher in 2008 (before grass carp stocking) than 2009 and 2010 (after grass carp stocking). Changes in PSD and PSD-P were observed in several other vegetation control projects. In Guntersville Reservoir, Wrenn et al. (1994) reported a decline in largemouth bass PSD and PSD-P after submerged vegetation control. Mallison et al. (1994) reported increases in largemouth bass PSD from 37% to 62%, and PSD-P from 10% to 30%, two years after grass carp stocking. Bluegill PSD and PSD–P were not reported in any literature pertaining to vegetation control projects. Decreases in PSD in 2009 and 2010 could be a result of the strong 2008 and 2009 year classes. Many of those fishes would have been approximately stock size in 2009 and 2010. Their presence in samples would have resulted in increases in the relative proportions of smaller fish in the bluegill and largemouth bass populations. Hence, PSD and PSD-P would have gone down, because of a larger number of small fish, not because of a smaller number of large fish.

Conclusions about the effects of large-scale vegetation control on sportfish population dynamics and characteristics are conflicting. The relationship between fishes and vegetation can be influenced by system morphology and water depth (Hoyer and Canfield 1996). Felsenthal National Wildlife Refuge, a bottomland hardwood forest, is actually a riparian wetland (King et al. 1998) occurring along the Ouachita and Saline rivers and several tributary streams. The majority of the Felsenthal Reservoir is littoral area less than 1 m in depth (Olive et al 2010). Degree of habitat complexity may weaken relations between plants and fishes, making the relations difficult to discern and detect. Furthermore, spring water levels can heavily influence spawning success (i.e., recruitment) and other dynamics of centrarchid populations independent of submerged vegetation abundance. Because the Ouachita and Saline rivers are relatively unregulated, water level fluctuations in the Felsenthal Reservoir in some years (such as 2009) can be large.

Other large-scale vegetation control projects, such as Guntersville Reservoir, Lake Conroe, and Lake Marion, were conducted in reservoirs established for drinking water, commercial navigation, and hydroelectric power production (Klussman et al. 1988; Kirk and Henderson 2006; Webb et al. 1994). In general, these reservoirs were less complex, and comprised of mostly open water habitats where sportfish and other changes may have been more easily detected. Finally, relationships between predator and prey fishes would be expected to be more complex in larger reservoirs with richer fish communities compared to smaller lakes or ponds with fewer fish species (Killgore et al. 1998). Felsenthal Reservoir has a rich fish community. Largemouth bass are not the only piscivorous predator and bluegill not the only zooplanktivore. These species are components of a diverse fish community that includes gars, bowfins, gizzard shad, and multiple centrarchid species. Thus, changes in the largemouth bass population would be expected to have a less direct effect on the bluegill population in Felsenthal Reservoir than compared to smaller, simpler systems. It is possible other characteristics of Felsenthal Reservoir that were not measured may have contributed significantly to the observed changes in sportfish populations characteristics than vegetation control. Hence, changes in sportfish population characteristics following vegetation control may not be as straightforward in the Felsenthal Reservoir as in some other studies.

Management Implications

Reduction of nuisance submerged vegetation generally leads to increased angler visits and increased angler satisfaction. Fishing visitors in FNWR increased by 63% from 2008 to 2010 after the stocking of grass carp (USFWS 2010; Figure 16). According to largemouth bass anglers in FNWR, largemouth bass catch rates also increased following reduction in submerged vegetation (Kyle Browning, local angler, personal communication). In Washington, Bonar et al. (2002) reported increased property owner satisfaction when aquatic vegetation was controlled. Bonar et al. (2002) reported quality of landowner recreation activities increased 63% after grass carp stocking. However, Bonar et al. (2002) also reported 71% of landowners saw no change in angling quality, after grass carp stocking. In South Carolina, Henderson et al. (2003) reported 21% of bank anglers and 15% of boat anglers thought control of aquatic vegetation helped fishing success. Control of submerged aquatic vegetation can benefit recreational user groups and landowners, and improve the socioeconomic value of a water body and fishery (Henderson et al. 2003). However, consideration of all the impacts, values, and perceptions of user groups should be viewed before implementation of an aquatic plant management project.

By monitoring system responses to management activities, fisheries managers gain a better understanding of how their decisions affect a fishery and its user groups.

Monitoring enables fisheries managers to do their job better, because it allows them to adjust decisions and policies as more information becomes available. By monitoring the change in aquatic vegetation percent coverage and biomass in FNWR, managers gained a better understanding of the techniques needed to control nuisance vegetation in order to balance sport fisheries needs (e.g., enhanced size structure or angler catch) and recreational needs (e.g., open boating lanes and enhance backwater access). Monitoring is especially important in complex systems, which often respond to management actions in unintended and unexpected ways. Through further monitoring of the largemouth bass and bluegill population characteristics in FNWR and the vegetation community, fisheries managers will gain a better understanding of the management and conservation actions needed to sustain this valuable sport fishery.

Grass carp are a long-term solution to control of nuisance of submerged vegetation in FNWR. However, more research is needed to investigate the direct and indirect impacts of grass carp on all ecological impacts. Future investigations need to quantify the impacts across aquatic and terrestrial vegetation species and vegetated habitats. Which are essential for understanding habitat changes and the effects of changing the habitat may play on the aquatic and terrestrial vegetation communities. Additional information is also required to determine how grass carp influences multi-species interactions like predator-prey interactions, trophic interactions, and competition. Additional information on how grass carp influence individual behaviors like foraging efficiency, predator avoidance, and habitat use would be useful. Future investigations need to encompass all ecological impacts on the environment in which grass carp are stocked, because what may be beneficial to one aspect of the ecosystem may have negative effects on another. Until all of the effects of grass carp on the ecology of an ecosystem are examined, conservation of that ecosystem can never fully be maintained.

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TABLES

Table 1. –Location, latitude, and longitude of exclusion cages.

Location	Latitude	Longitude
Pete Wilson	33° 4'18.83"N	92° 6'25.67"W
First Flatwater	33° 4'55.11"N	92° 7'4.04"W
Second Flatwater	33° 5'33.50"N	92° 7'20.29"W
Wildcat Lake	33° 6'12.24"N	92° 6'29.13"W
Bull Brake	33° 4'36.56"N	92° 6'9.32"W
Grand Marias	33° 3'36.10"N	92° 7'53.14"W
Dollar Slough	33° 4'25.01"N	92° 9'25.54"W
Shallow Lake	33° 6'31.76"N	92° 8'38.78"W
Fish Trap Lake	33° 8'13.01"N	92° 9'29.35"W
Open Brake	33° 7'33.12"N	92° 8'14.50"W

Table 2. –Bioenergetics parameters entered into Wisconsin Bioenergetics Model 3.0. Parameter values and justification for setting parameter values.

Parameters	Value	Justification
Individual & Population		
Simulation start day:	1	18-Nov-2008
Simulation final day:	365	17-Nov-2009
P-estimate and run start weight (g):	127- 353	Varied
P-estimate final weight (g):	1,400-3,156	Varied
Estimated P-value:	Varied	Calculated by program
Run P-value:	Varied	Calculated by program
Initial population:	1	Individual Consumption
Simulation Setup		
Consumption model:	1	Default for tilapia
Egestion model:	0	Default for tilapia
Predator cal model:	0	Default for tilapia
Respiration model:	1	Default for tilapia
Spawn (T/F):	F	Default for tilapia
Mortality (T/F):	F	Default for tilapia
Use predator energy density file (T/F):	T	Default for tilapia
Contaminant analysis (T/F):	F	Default for tilapia
Nutrient analysis (T/F):	F	Default for tilapia
Constant method:	0	Default for tilapia
P-value method:	0	Default for tilapia
Maintenance temperature:	17.1	Wiley and Wike 1986
P-value or constant ration during run:	0	Default for tilapia
Input Data Files		
Diet proportions:	1	100% diet of hydrilla
Prey energy density (J/g wet weight):	1,330	Cummins and Wuycheck 1971
Temperature (^{o}C):	5 - 30.5	MicroDat Data Logger
Predator energy density (J/g wet weight):	5,639	Reagan 1969
Consumption		
Ca:	1.7	Kilambi and Robison 1979
Cb:	-0.1	Kilambi and Robison 1979
Ck1:	0	Default for tilapia
Ck4:	0	Default for tilapia
Cq:	2.5	Default for tilapia
Ctl:	0	Default for tilapia

Table 2. –(cont.)

Parameters	Value	Justification
Ctm:	37	Kilambi and Robison 1979
Cto:	23.8	Kilambi and Robison 1979
Eq:	2	Default for tilapia
Ration:	0	Default for tilapia
Egestion & Excretion		
Eq:	1	Default for tilapia
Fa:	0.36 - 0.60	Varied at 0.04 Increments
Fb:	0	Default for tilapia
Fg:	0	Default for tilapia
Ua:	0.11	Carter and Brafield 1992a
Ub:	0	Default for tilapia
Ug:	0	Default for tilapia
Predator Caloric Density		
Alpha1:	0	Default for tilapia
Alpha2:	0	Default for tilapia
Beta1:	0	Default for tilapia
Beta2:	0	Default for tilapia
Cal:	5,639	Reagan 1969
Cutoff:	0	Default for tilapia
Eq:	1	Default for tilapia
Cutoff:	0	Default for tilapia
Respiration		
Act:	2 - 3	Variable
Bact:	0	Default for tilapia
Eq:	2	Default for tilapia
Ra:	0.17	Carter and Brafield 1992a
Rb:	-0.35	Carter and Brafield 1992a
Rk1:	0	Default for tilapia
Rk4:	0	Default for tilapia
Rq:	2.3	Default for tilapia
Rt1:	0	Default for tilapia
Rtm:	41	Default for tilapia
Rto:	37	Default for tilapia
Sda:	0.1	Default for tilapia

Table 3. –Mean (SD) width and percent coverage of emergent vegetation before and after herbicide application in July of 2008. Herbicide was applied in three locations (Mahoney Channel, Grand Marias, and Open Brake). Mean widths and percent coverages are averages of three transects per location.

		Location		
Metric	Period	Mahoney Channel	Grand Marias	Open Brake
Width (m)	Before	44.7 (38.1)	91.3 (57.6)	127.3 (10.5)
	After	0.0	0.0	0.0
Percent coverage (%)	Before	65.0 (47.7)	83.3 (7.6)	64.3 (29.3)
	After	0.0	0.0	0.0

Table 4. –Mean (SD) percent coverage and biomass in 2008 and 2010. Grass carp stocking occurred in late 2008, following the preliminary vegetation survey.

Year	Percent Coverage (%)	Biomass (g/m^2)
2008	11.5 (28.7)	57.8 (157.2)
2010	33.3 (45.8)	138.1 (346.5)

Table 5. –Mean (SD) biomass of dominant vegetation in 2008 and 2010. Grass carp stocking occurred in late 2008, following the 2008 vegetation survey.

Year	Vegetation	Biomass (g/m^2)
2008	American lotus	23.7 (83.8)
	hydrilla	20.5 (86.2)
	egeria	6.3 (45.4)
	coontail	5.4 (27.1)
	duckweed	1.4 (9.2)
2010	American lotus	111.8 (286.6)
	fragrant water lily	25.3 (206.8)
	coontail	0.5 (4.1)
	duckweed	0.2 (0.4)
	hydrilla	0.1 (0.3)

Table 6. –Vegetation relative abundance by species and year. Grass carp stocking occurred in late 2008, following the 2008 vegetation survey.

	Year	
	2008	2010
Species	Relative abundance (%)	Relative abundance (%)
American lotus	41.2	81.0
Hydrilla	35.6	0.1
Egeria	11.0	<0.1
Coontail	9.4	0.4
Duckweed	2.5	0.1
Frogs bit	0.2	<0.1
Fanwort	0.1	0.1
Slender naiad	0.1	<0.1
Fragrant water lily	<0.1	18.3
American pondweed	<0.1	<0.1

Table 7. –Biomass and relative abundance by vegetation type. Vegetation is categorized as submerged or floating/emergent. Submerged vegetations include hydrilla, coontail, egeria, fanwort, slender naiad, and American pondweed. Emergent/floating vegetations include duckweed, American lotus, frogs-bit, and fragrant water lily.

	Year			
	2008		2010	
Vegetation type	Biomass (g/m^2)	Relative abundance (%)	Biomass (g/m^2)	Relative abundance (%)
Submerged	2233.5	56.2	52.0	0.6
Floating/emergent	1741.0	43.8	9476.0	99.4

Table 8. -Percent similarity of vegetation community before and after grass carp stocking, based on two different data sources.

Data Source	Percent Similarity
Percent Coverage	58
Biomass	42

Table 9. –Vegetation biomass inside and outside of exclusion cages. Mean (SD) biomasses of hydrilla, American lotus and total vegetation inside and outside of exclusion cages are included in the last row.

	hydrilla biomass (g/m^2)		American lotus biomass (g/m^2)		Total biomass (g/m^2)	
Location	inside	outside	inside	outside	inside	outside
Pete Wilson	2,000	0	264	8	2,264	8
First Flatwater	503	0	1,854	437	2,357	437
Second Flatwater	0	1	0	0	0	1
Wildcat Lake	0	0	0	0	0	0
Bull Brake	0	0	0	0	0	0
Grand Marias	26	0	500	318	526	318
Dollar Slough	2,275	3	0	0	2,275	3
Shallow Lake	6	0	0	0	6	0
Fish Trap Lake	0	0	0	0	0	0
Open Brake	2,026	1	12	0	2,038	1
Mean (SD)	1139.5 (1072.5)	2.3 (1.4)	658.2 (822.3)	254.5 (221.8)	1578.4 (1035.6)	128.1 (197.7)

Table 10. –Parameters used to calculate the ratio of annual hydrilla consumption by all stocked grass carp to annual hydrilla production (C:P ratio) for the Felsenthal National Wildlife Refuge.

Parameter	C:P ratio Maximum	Median	Minimum
Individual Consumption			
Initial weight of a grass carp in 2008 (g)	127	226	353
Final weight of a grass carp in 2009 (g)	3,156	1,992	1,400
Annual weight gain of a grass carp (g fish flesh/year)	3,029	1,766	1,047
Conversion ratio (g vegetation/g fish flesh)	94	71	48
Annual individual consumption (g vegetation/year)	284,726	125,386	50,256
Population Mortality			
Grass carp stocked by end of 2008	67,677	67,677	67,677
Total annual mortality (%)	1	17	33
Population Consumption			
Annual population consumption (g vegetation/year)	1.92E+10	7.70E+09	2.79E+09
Refuge area (m^2)	40,470,000	40,470,000	40,470,000
Area specific consumption ($g \cdot m^{-2} \cdot year^{-1}$)	474	190	56
Vegetation Production			
Area specific hydrilla production ($g \cdot m^{-2} \cdot year^{-1}$)	6.4	16.0	2,275.6
C:P Ratio	73.99	11.90	0.03

Table 11. –Comparison of annual individual consumption using conversion ratios from literature and Wisconsin Bioenergetics Model 3.0.

	Weight gain		
	Maximum	Median	Miminum
Modeling method	Annual individual consumption (g vegetation/year)	Annual individual consumption (g vegetation/year)	Annual individual consumption (g vegetation/year)
Conversion ratios from literature	284,726	125,386	50,256
Wisconsin Bioenergetics Model	150,991	148,651	151,913

Table 12. –Sensitivity analysis of uncertain parameters of Wisconsin Bioenergetics Model 3.0. Annual individual consumption for median case (top row) was calculated using at median values for all parameters. Uncertain parameters of weight gain, activity, egestion (Fa), and critical thermal optimum were modeled at ± 25%, ± 25%, ± 24%, and ± 25% around the median, respectively. Percent difference was calculated by dividing median annual individual consumption from each varied parameter by median annual individual consumption from the median case.

Weight gain	Activity	Egestion (Fa)	Critical thermal optimum (ºC)	Annual individual consumption (g vegetation/year)	% Difference
1,766	2.5	0.48	23.8	148,651	-
1,766	2.0	0.48	23.8	119,135	-19.9
1,766	3.0	0.48	23.8	179,657	20.9
1,766	2.5	0.36	23.8	120,779	-18.8
1,766	2.5	0.60	23.8	193,249	30.0
1,766	2.5	0.48	18.3	260,394	75.2
1,766	2.5	0.48	29.4	92,975	-37.5
2,208	2.5	0.48	23.8	130,356	-12.3
1,324	2.5	0.48	23.8	154,187	3.7

Table 13. –von Bertalanffy growth curve equation coefficients for bluegill. Parameters of L_{∞}, k, and t_0 with upper (UCL) and lower (LCL) 95% confidence limits.

Time	L_{∞}	LCL	UCL	k	LCL	UCL	t_0	LCL	UCL
2008	284.0	150.5	417.5	0.176	0.016	0.336	-1.91	-2.70	-1.11
2009	234.9	200.1	269.7	0.375	0.215	0.535	-1.19	-1.57	-0.81
2010	430.9	84.3	777.5	0.107	-0.016	0.230	-1.46	-2.03	-0.89

Table 14. –von Bertalanffy growth curve equation coefficients for largemouth bass. Parameters of L_{∞}, k, and t_0 with upper (UCL) and lower (LCL) 95% confidence limits

Time	L_{∞}	LCL	UCL	k	LCL	UCL	t_0	LCL	UCL
2008	475.5	368.3	582.8	0.298	0.154	0.442	-1.18	-1.49	-0.87
2009	481.3	435.1	527.6	0.543	0.382	0.704	-0.55	-0.78	-0.31
2010	966.4	363.0	1569.9	0.114	-0.019	-0.209	-0.82	-1.09	-0.54

FIGURES

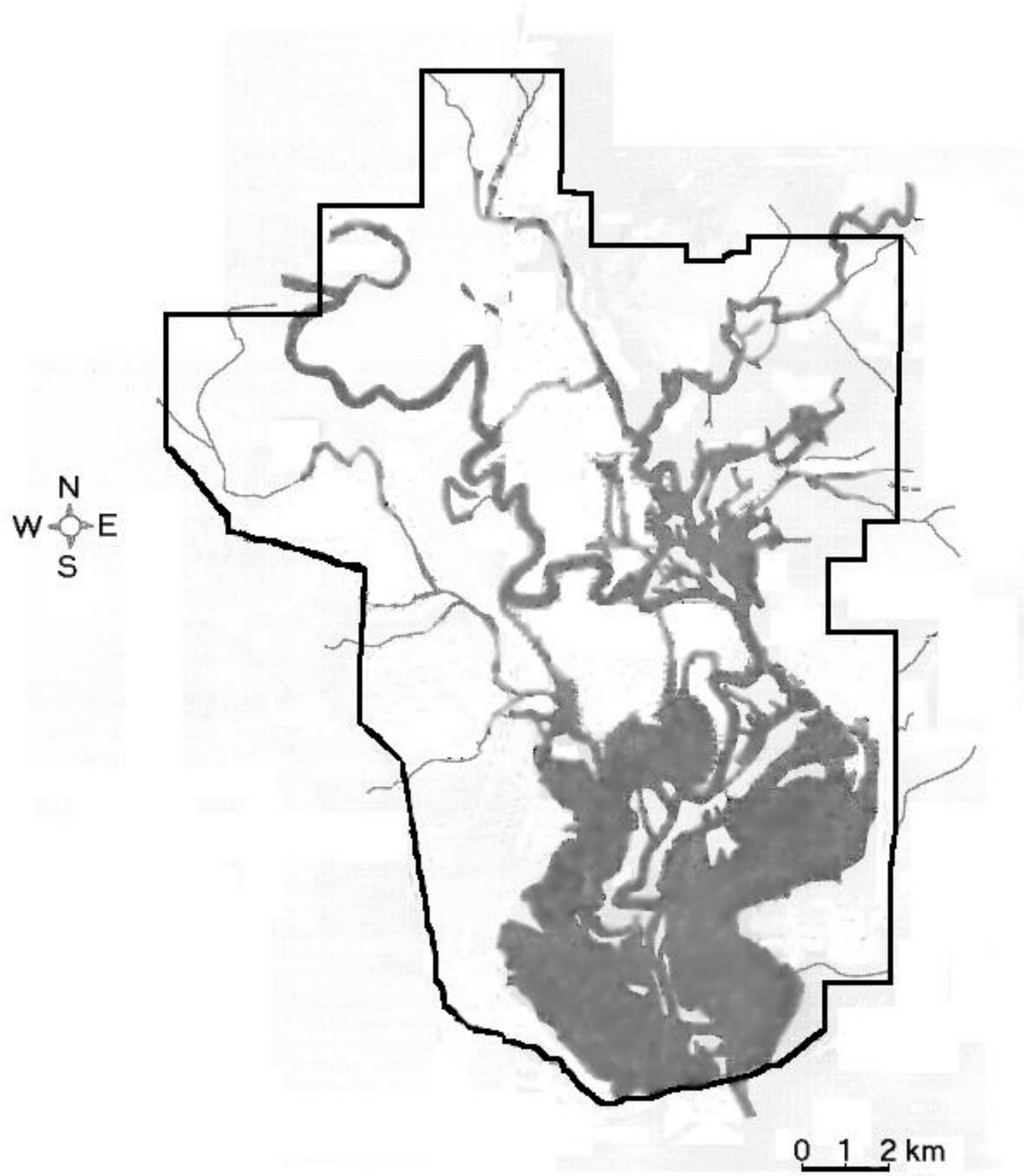

Figure 1. –Map of Felsenthal National Wildlife Refuge.

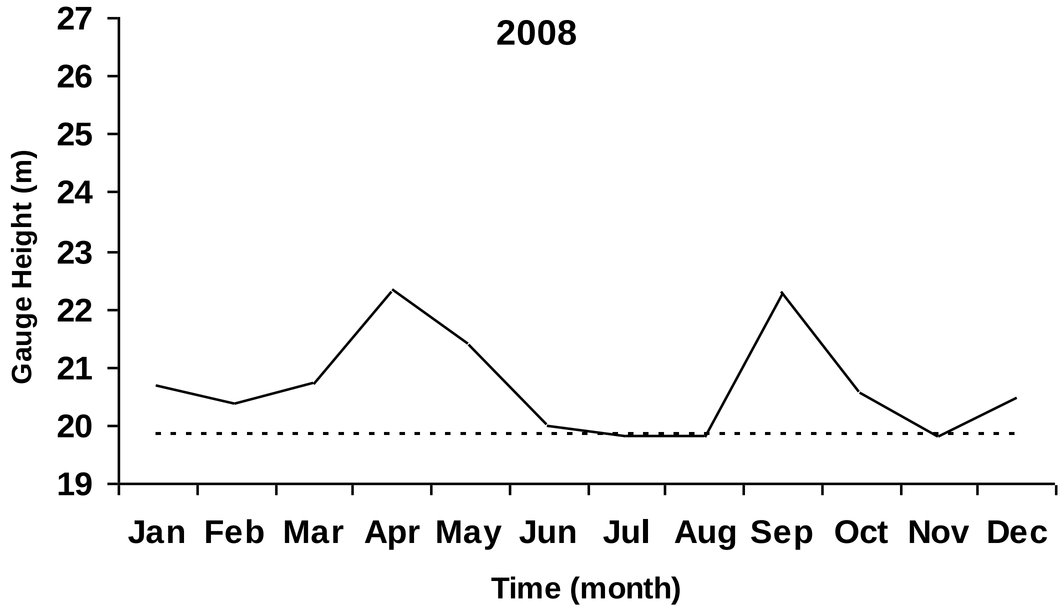

Figure 2. –Hydrology of Felsenthal National Wildlife Refuge in 2008. Dotted line represents conservation depth of 19.8 m.

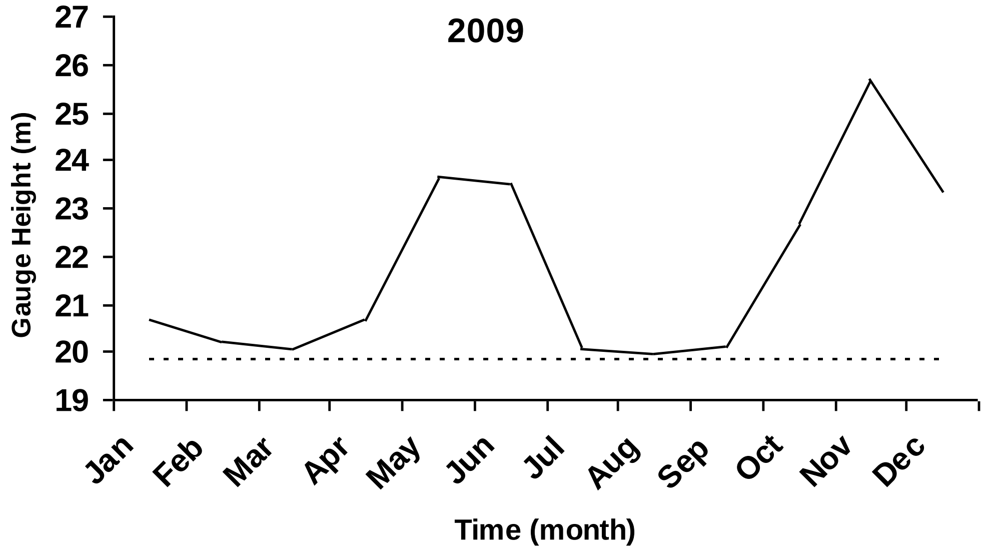

Figure 3. –Hydrology of Felsenthal National Wildlife Refuge in 2009. Dotted line represents conservation depth of 19.8 m.

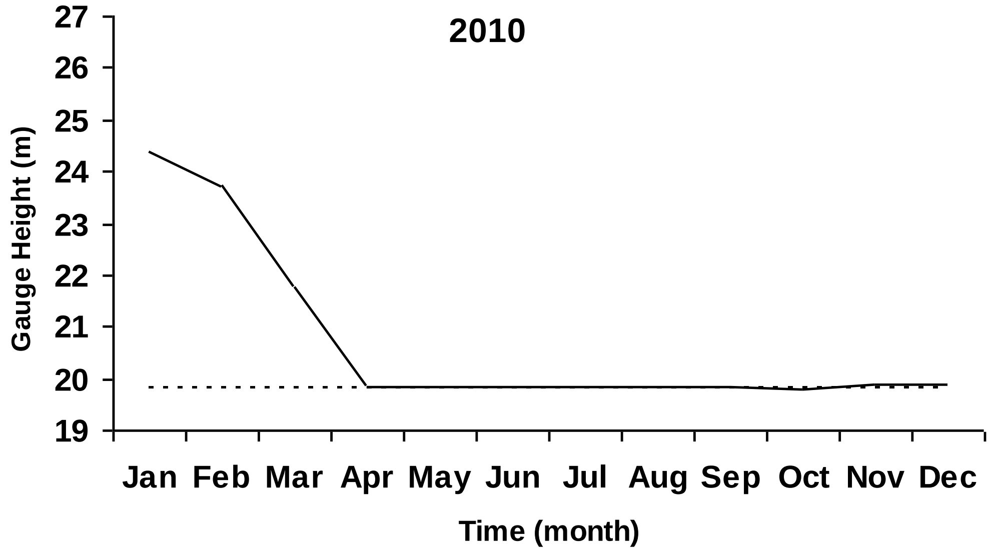

Figure 4. –Hydrology of Felsenthal National Wildlife Refuge in 2010. Dotted line represents conservation depth of 19.8 m.

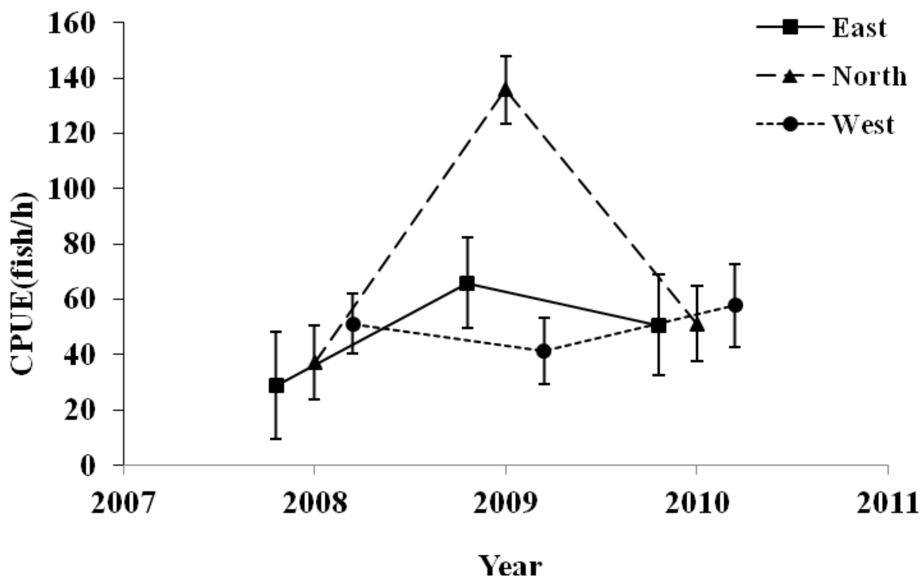

Figure 5. –Mean and standard deviation bluegill catch per unit effort (CPUE). Catch per unit effort calculated as fish/h of electrofishing.

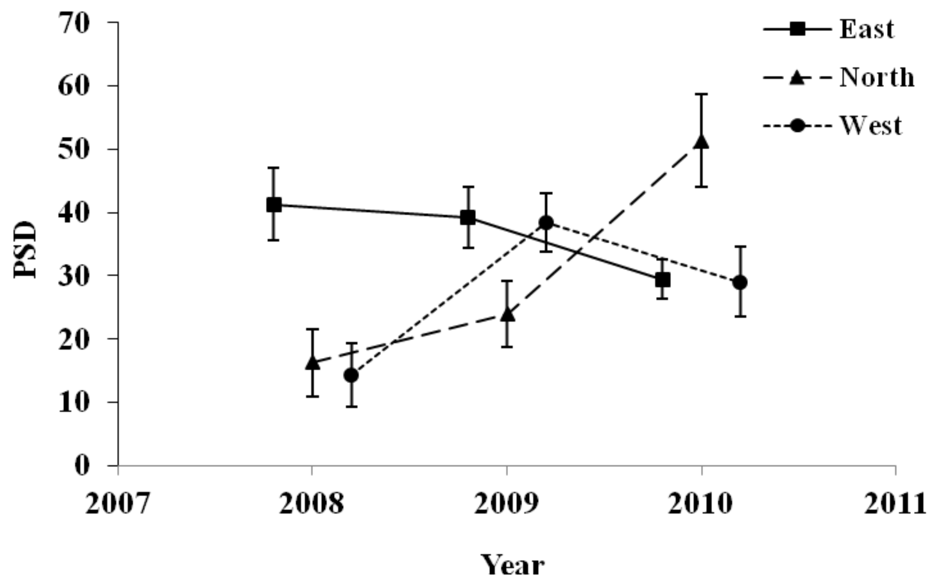

Figure 6. –Mean and standard deviation bluegill proportional size distribution of quality size fish (PSD).

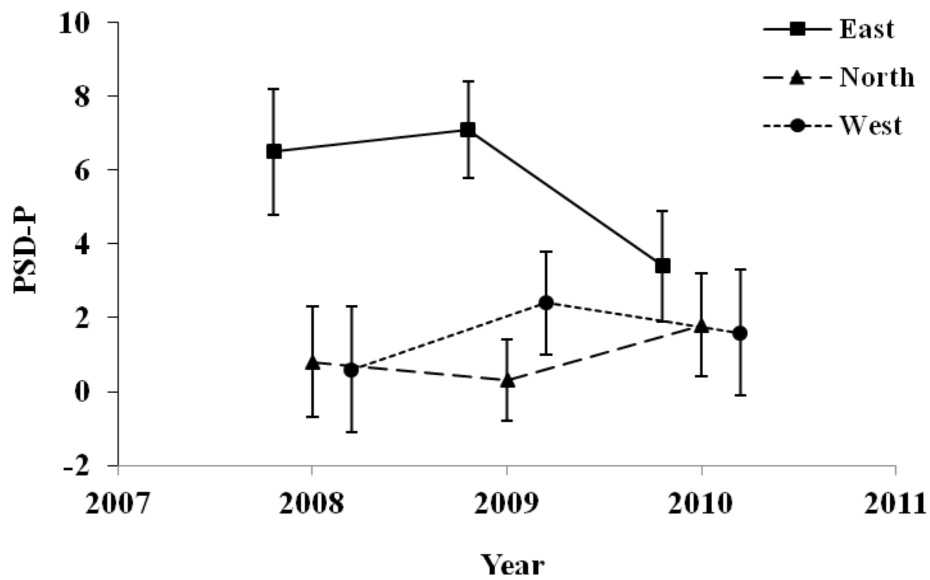

Figure 7. –Mean and standard deviation bluegill proportional size distribution of preferred size fish (PSD-P).

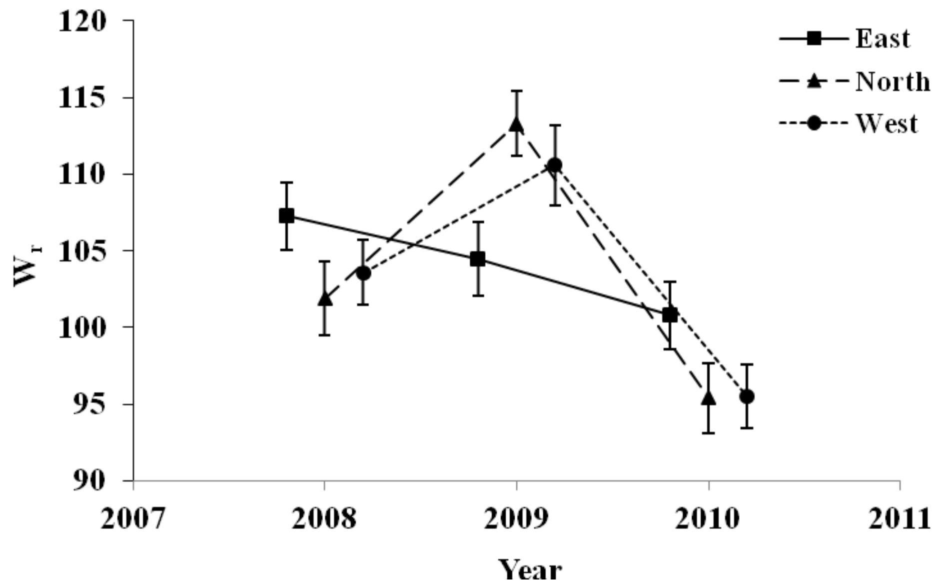

Figure 8. –Mean and standard deviation bluegill relative weight (W_r).

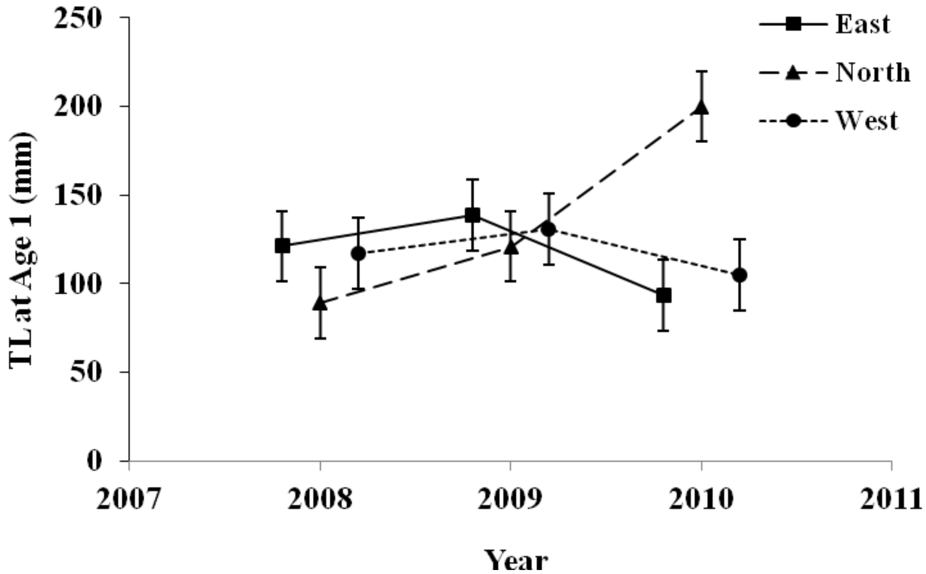

Figure 9. –Mean and standard deviation bluegill TL (mm) at age 1.

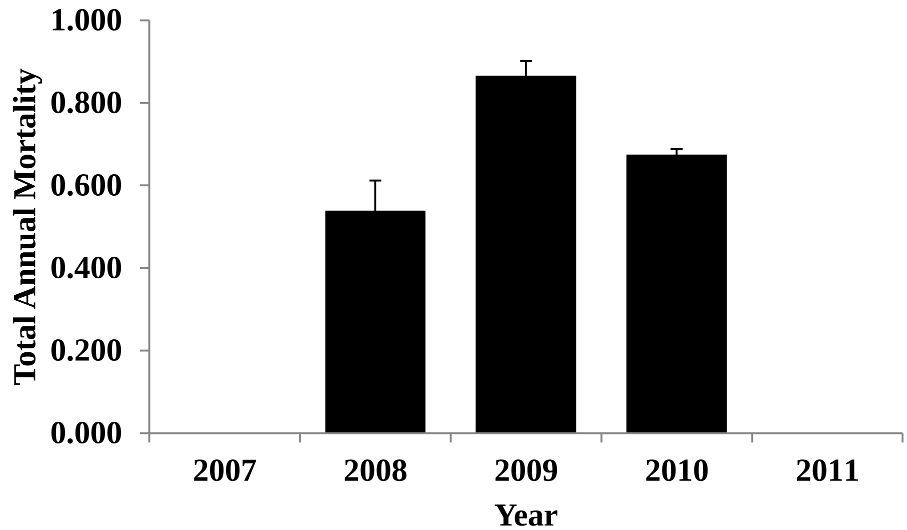

Figure 10. –Bluegill total annual mortality (A) and standard deviation. Years with the same letter were not significantly different.

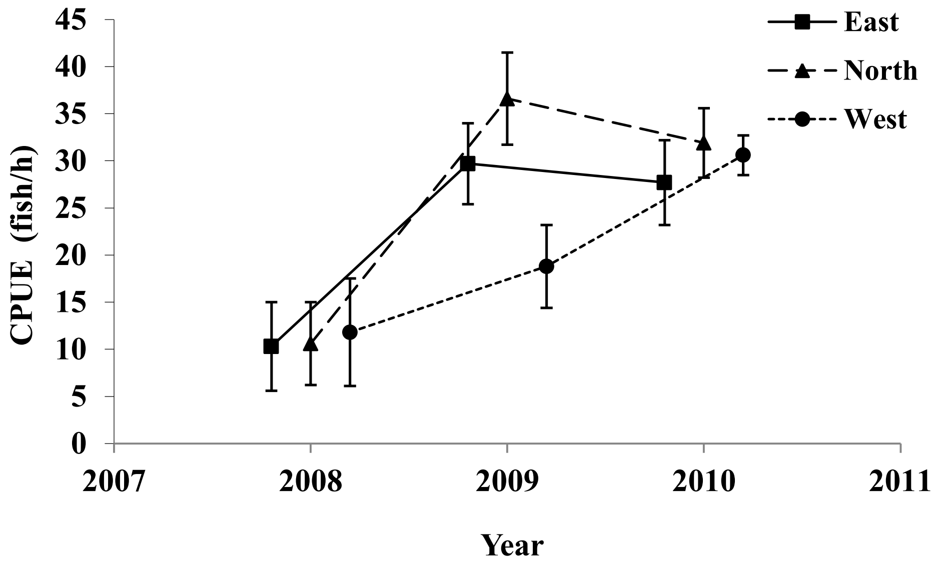

Figure 11. –Mean and standard deviation largemouth bass catch per unit effort (CPUE). Catch per unit effort calculated as fish/h of electrofishing.

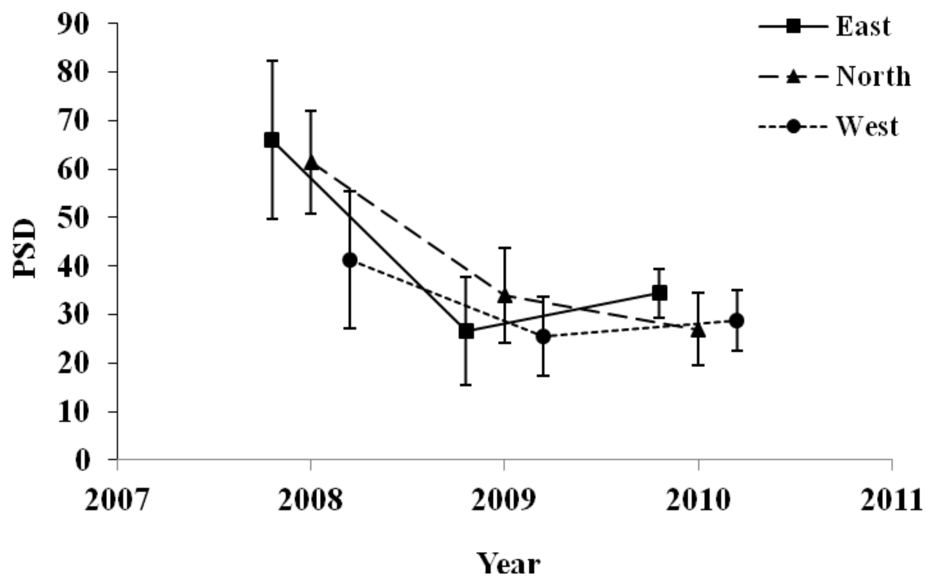

Figure 12. –Mean and standard deviation largemouth bass proportional size distribution of quality size fish (PSD).

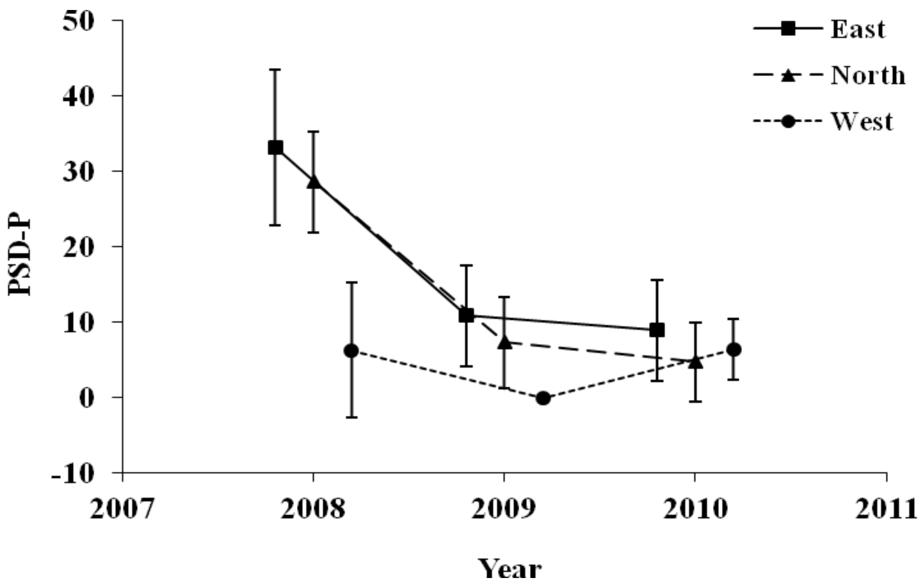

Figure 13. –Mean and standard deviation largemouth bass proportional size distribution of preferred size fish (PSD-P).

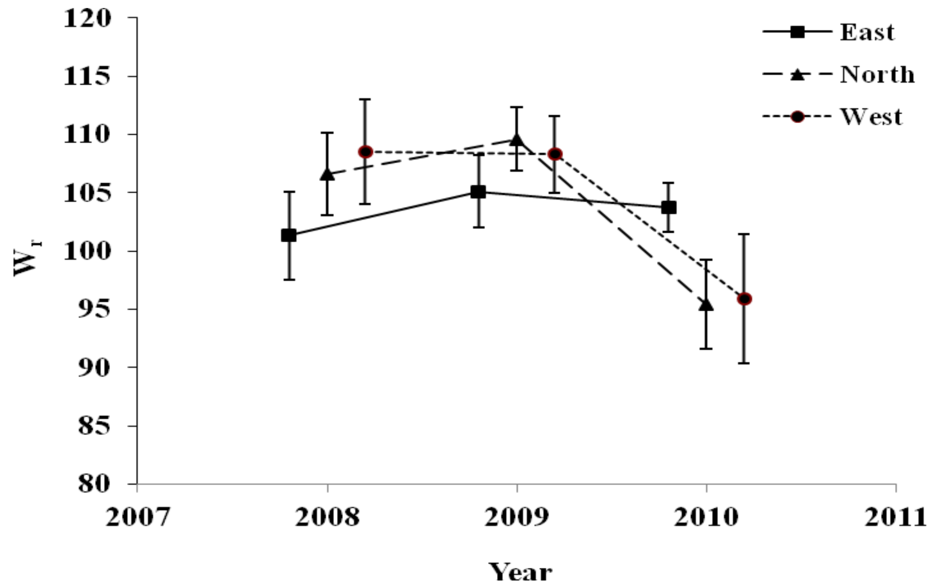

Figure 14. –Mean and standard deviation largemouth bass relative weight (W_r).

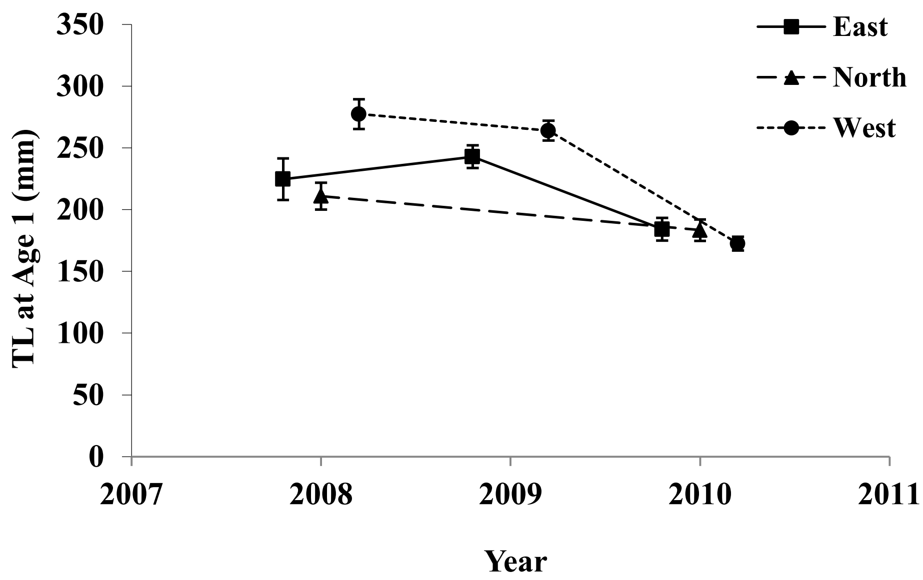

Figure 15. –Mean and standard deviation largemouth bass TL (mm) at age 1.

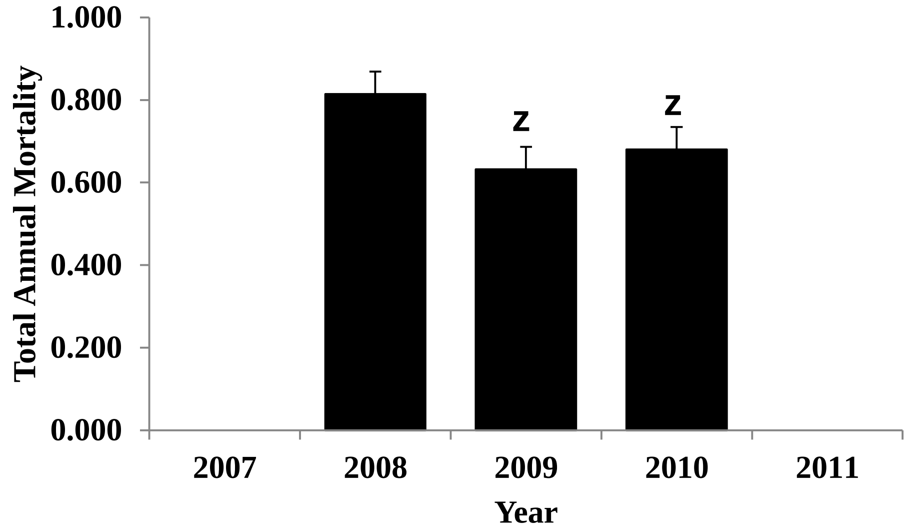

Figure 16. –Largemouth bass total annual mortality (A) and standard deviation. Years with the same letter were not significantly different.

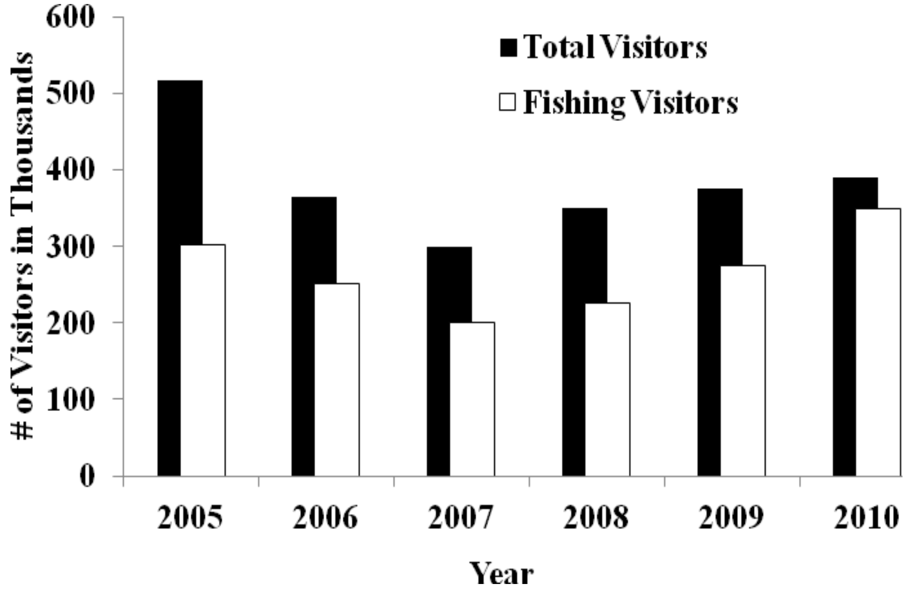

Figure 17. –Number of total visitors and fishing visitors (in thousands) to the Felsenthal National Wildlife Refuge from 2005 to 2010.