

BEHAVIOR AND POPULATION DYNAMICS OF GRASS CARP INCREMENTALLY
STOCKED FOR BIOLOGICAL CONTROL

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Behavior and population dynamics of grass carp incrementally stocked for biological control

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Abstract: Grass carp *Ctenopharyngodon idella* have been stocked throughout the world due to their utility as a biological control. In the United States, the species has been used to successfully control invasive, aquatic weeds such as hydrilla *Hydrilla verticillata*. Despite the large body of research surrounding the use of grass carp, few studies have demonstrated widely applicable methods for evaluating the success of weed control based on grass carp behavior and population dynamics. Classic methods of biological control using grass carp often rely on a single, large stocking of fish. Few of these studies have demonstrated success in achieving intermediate levels of weed control. Managers would be better equipped to make decisions regarding stocking and maintenance grass carp populations with better information about behavior, survival, and population structure. Improved decision making could result in reduced cost and increased effectiveness of stocking. In order to examine current knowledge gaps for management, I investigated the movements and habitat use of grass carp, post-stocking survival, age-specific survival rates, and population dynamics of grass carp in Lake Gaston, North Carolina and Virginia.

I characterized relationships between grass carp behavior and environmental factors using radio-telemetry. The average rate of movement for grass carp in Lake Gaston was about 137 m/d. Rapid dispersal after stocking was followed by long periods of no movement. However, when time after stocking was held constant in models of behavior, fish moved about 200 m/d

more in the second year after stocking than in the first year, and were found closer to shore. On average, grass carp were found about 40 m from shore in about 2.5-3.5 m of water, although mean depth of water at grass carp locations varied seasonally, being shallowest in summer and deepest in winter. Although depth of water at grass carp locations did not vary by stocking location, Grass carp were found closer to shorelines in the upper reservoir than in the lower reservoir. I found significant relationships between grass carp behavior and hydrological processes such as lake elevation and dam releases in the reservoir, as well as with other environmental factors such as water temperature, photoperiod, and weather conditions. The results of this study should be useful in better understanding how behavior can affect management decisions. Specifically, grass carp behavior appears to change with age and environmental conditions within large reservoir systems. Future research should focus more closely on the effects of large-scale flow dynamics on grass carp behavior.

I estimated age-1 survival of grass carp from mark-recapture models designed for radio-tagged animals, and characterized relationships between age-1 survival and factors under the control of management, such as stocking locations and size at stocking. According to the most-plausible model developed in this study, survival of age-1 grass carp in Lake Gaston varied throughout the year, and the probability of an individual grass carp surviving to the end of its first year (\pm SE) was $0.57(\pm 0.10)$. According to the second-most-plausible model developed in this study, grass carp survival varied between stocking locations, and was twice as high in the upper reservoir (0.87 ± 0.09) than in the lower reservoir (0.43 ± 0.11). The differences in survival between stocking locations suggest that the cost-effectiveness of grass carp stocking could be improved by focusing stocking efforts in specific regions of Lake Gaston. Furthermore, none of the models developed in this study that incorporated the effects of size (length and weight) or

condition factor accounted for a meaningful amount of the total model weights. These results suggest that costs of grass carp stocking could be reduced in Lake Gaston by using a smaller minimum size (352 mm, TL) than is commonly referred to in the literature (450 mm, TL). I used grass carp collected by bowfishers in Lake Gaston to characterize the age, growth, and survival of grass carp in the system. From these data, I characterized relationships between fish population dynamics and annual hydrilla coverage. Grass carp collected from Lake Gaston ranged in age 1-16 years. Growth of grass carp in Gaston was described by the von Bertalanffy growth function as $L_t = 1297(1 - e^{-0.1352(t+1.52)})$. I estimated mortality from the von Bertalanffy growth parameters using methods based on growth, temperature, and age; and with each mortality estimate I estimated population size and standing biomass of grass carp. Use of age-specific mortality rates produced lower estimates of grass carp numbers and standing biomass in Lake Gaston than did the use of a single, instantaneous mortality rate for all ages. I determined that growth of grass carp slowed considerably after the fourth year and that slowed growth, in combination with changes in mortality, resulted in a decrease in the amount of hydrilla controlled by a given cohort after four years in Lake Gaston. This phenomenon resulted in an approximately linear relationship between the biomass of grass carp at year i and hectares of hydrilla at year $i+3$. Based on this relationship, I predicted that the biomass of grass carp necessary to reduce hydrilla coverage to the target level of 120 ha in Lake Gaston is about 91,184 kg ($\pm 38,146$ kg) and that the current biomass of grass carp in Lake Gaston is about 108,073 kg ($\pm 3,609$ kg). I conclude that grass carp biomass is at or near levels that should reduce hydrilla coverage to 120 ha between 2013 and 2018. This research provides an effective means for synthesis of information that is critical to understanding sterile, triploid grass carp populations when assumptions of other methods cannot be met. The results of this study should

be of immediate utility to hydrilla management efforts in Lake Gaston and other systems.

Furthermore, the age-specific mortality rates developed in this study should be useful as starting values for grass carp management in similar systems.

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Chapter 1: Introduction

Introduction

Hydrilla: a global problem

Hydrilla *Hydrilla verticillata* is a highly invasive aquatic weed that belongs to the family Hydrocharitaceae. Hydrilla is a rooted macrophyte (Pons 2005), occurring in water as deep as 15 m (Yeo et al. 1984). It grows long, thin shoots that form thick mats when they reach the surface during summer and autumn (Haller and Sutton 1975; Colle and Shireman 1980; Pons 2005; MacDonald et al. 2008). Hydrilla is native to Australia (Swarbick et al. 1981), Asia, and Central Africa (Cook and Luond 1982; Madiera et al. 2007). The plant now occurs on every continent but Antarctica (Shabana et al. 2003) in both saltwater and freshwater (Evans et al. 2007). These introductions are largely viewed as human-induced phenomena (Mitchell and Kelly 2006; Binimelis et al. 2007).

Hydrilla is a highly adaptable plant (Madiera et al. 2007), and it has tremendous reproductive potential (Langeland 1990; Pons 2005; Puri et al. 2007). Low water levels and high summer temperatures favor rapid hydrilla growth (Haller et al. 1980). Hydrilla produces propagules in the form of tubers that can persist in sediment for up to seven years and turions (perennial buds) that lay dormant from fall to spring (Hofstra et al. 1999). A single turion can form up to 16 shoot tips (Langeland and Sutton 1980; MacDonald et al. 2008). If unchecked, the result of a hydrilla infestation is most often a dense monoculture (Olsen et al. 1998).

Problems created by hydrilla infestation include obstruction of waterways and pipelines, interference with recreational uses of water, and adverse ecological impacts. As the economic costs of environmental damage caused by invasive species nears USD\$120 billion per year in the United States, it is less expensive to control the weed than to let it spread (Pimentel et al. 2005).

For example, angler effort decreased 90% following hydrilla infestation in Orange Lake, Florida which supported a sport fishery valued at \$1 million (Colle et al. 1987).

Proposed controls for hydrilla

Three broad classes of weed management techniques exist: mechanical, chemical, and biological controls (Schramm and Brice 1998). Mechanical control requires the greatest amount of investment and engineering (Hanlon et al. 2000). Examples of mechanical control include biomass harvesting, dredging, drawdown, and bottom sealing. Biomass harvesting is expensive and time consuming, but is the most common method of mechanical control. The cost of biomass harvesting can easily exceed \$1,000 per hectare (McGehee 1979). It often results in the removal of non-target flora and fauna (Wile 1978; Mikol 1985; Engel 1990; Booms 1999). Mechanical harvest resulted in the physical removal of 32% of fish by number and 18% of fish biomass from harvested areas in a 5,000-ha lake in Florida (Haller et al. 1980). The estimated cost to replace the lost biomass was \$6,000 per hectare.

Herbicide applications can effectively control hydrilla infestations for at least twice as long as mechanical harvesting (Fox and Haller 1992). However, chemical control can also be expensive (Shireman 1982; Hanlon et al. 2000), costing more than \$875 per hectare (Maceina et al. 1999; Kirk and Henderson 2006). Fluridone (SONAR) is the only USEPA-approved herbicide that effectively controls hydrilla in whole-lake applications (Puri et al. 2007). One limitation of fluridone is that plant death often requires long contact times or high temperatures (Hofstra and Clayton 1999). Long herbicide-contact times or high levels of herbicide application exert strong selection pressure that can expose herbicide resistance in weeds in just a few

generations (Michel et al. 2004; Pons 2005; Zajicek 2008). Reliance on one herbicide has recently led to instances of resistance in hydrilla populations within the U.S. (Richardson 2008).

Biological controls are an alternative to chemical and mechanical methods of weed control in aquatic systems (Mitchell and Kelly 2006). The most frequently used biological controls are insects, pathogens, and vertebrate animals. However, most management plans that use host-specific insects and pathogens have been limited in long-term success (Byrne et al. 2003). One potential solution to problems associated with various control measures is the combination of chemical and biological controls. For example, a fungal pathogen *Mycoleptodiscus terrestris* facilitates greater efficiency of herbicide treatments due to short-term stresses on the plant such as tissue damage (Netherland and Shearer 1996; Shearer 1998; Shabana et al. 2003). While the combined use of invertebrates and chemicals to control noxious weeds is gaining popularity, this technique faces many of the same challenges posed to individual use of either method, such as inadequate contact and long required retention times (Forno and Confrancesco 1993). A more-effective alternative might be to combine herbicide applications with an herbivorous fish.

Grass carp as a biological control

Grass carp *Ctenopharyngodon idella* are native to the Amur River, which flows from latitude 50°N to 23°N through Siberia, Manchuria, and China into the Pacific Ocean (Bailey and Boyd 1972). They are one of the largest cyprinid fishes, with recorded weights up to 181 kg (Chilton and Muoneke 1992), though they more typically reach weights of 30-36 kg in their native range. Growth rates in excess of 2.5 mm (and 14.9 g) per day have been recorded for the species (Mitzner 1978). Equipped with ridged, pharyngeal teeth, grass carp are well suited for

aquatic plant consumption (Prowse 1971), and may eat more than their weight in a day depending on fish age (Chilton and Muoneke 1992).

Grass carp feeding behaviors are well documented in the literature, and the fish appear to have hierarchical preferences for aquatic plants (Pine and Anderson 1991). Hydrilla is well documented as a preferred food of grass carp (Chilton and Muoneke 1992), and is one of the principal plant species that grass carp successfully control (Allen and Wattendorf 1987).

However, grass carp feeding preferences can be affected by factors other than plant species, such as fish size (Edwards 1974; Stott 1977; Sutton 1974; Van Dyke et al. 1984), temperature (Edwards 1974; Colle et al. 1978; Pine and Anderson 1989; Cai and Curtis 1990), plant texture (Kracko and Noble 1993), and accessibility of food (Pine and Anderson 1989; Pine et al. 1990). Energy content of plants does not necessarily determine food preference (Pine and Anderson 1991).

The results of reported efforts that use grass carp for hydrilla control have varied. Grass carp may completely eradicate vegetation in a water body through a single stocking (Stott and Robson 1970; Bettoli et al. 1993; Killgore et al. 1998; Schramm and Brice 1998). Conversely, they may not provide adequate control of vegetation with multiple stockings (Baker et al 1974; Kirk 1992; Killgore et al. 1998). Variability in potential impact has resulted in the use of stocking rates for grass carp that range from 2 to 500 fish per vegetated hectare (Kilgen and Smitherman 1971; Allen and Wattendorf 1987; Kirk et al. 2000; Bonar et al. 1993a, 2002).

An incremental approach to grass carp stocking may help managers to achieve an intermediate level of control, where vegetation is controlled at target levels and is not eradicated in a system (Chilton and Magnelia 2008). In incremental approaches, grass carp are stocked at low levels on a semi-annual basis. Stocking decisions are usually based on achieving a desired

number of fish per vegetated hectare. Target densities of grass carp may be adjusted through time based on the response of weed coverage to stocking efforts. Few studies have used this strategy when stocking grass carp for biological control of hydrilla (Chilton and Magnelia 2008). There are several factors influencing how many fish should be stocked, and how often. These factors have received relatively little attention in published studies, since most weed-control plans in the past have used a single, large stocking of grass carp.

Movement and habitat use of grass carp

One of the primary factors affecting the efficiency of noxious-weed control by grass carp is movement of fish to and from infested areas (Chilton and Poarch 1997). The most-effective control is achieved when grass carp remain in the system they are stocked in, and occupy target areas within that system (Nixon and Miller 1978). In their native range, grass carp have the potential to travel up to 500 km in their first two years of life (Gorbach and Krykhtin 1988). Due to the species' inclination to make long-distance migrations, emigration from target areas should be a primary consideration for stocking grass carp (Bain 1993; Maceina et al. 1999).

Life stage of the fish can be important in determining the effects of environmental factors on the movements and habitat use of grass carp. Temperature and growth rate also appear to be important in determining the size and age at which the fish become sexually mature (Kahn et al. 2004). These factors also may influence the behaviors of adult grass carp. However, few studies have sufficiently investigated the behavior of older grass carp. A minimum weight of 4.0 kg has been used to define adult grass carp for telemetry studies (Bain et al. 1990). Sexually mature grass carp moved greater distances than juveniles, and were not found in target areas as often (Bain et al. 1990). This behavior is similar to that described by Gorbach and Krykhtin

(1988), where juveniles remained downstream in the Amur River before migrating upstream as adults. Nixon and Miller (1978) observed movements of 12 grass carp for a period of only a few weeks. These are the only published accounts of adult grass carp movements, and the accounts of Bain et al. (1990) and Nixon and Miller (1978) are based on only 12 fish. Chilton and Poarch (1997) studied the movements of 69 grass carp of various sizes and indicated that core-use area and movement were both significantly and positively affected by stocking weight of grass carp. None of the above studies has followed individual fish for more than one year to determine relationships between movements and fish age. Technological advances in biotelemetry since the time of these studies allow for individual animals to be monitored for multiple years. By following a large number of fish for multiple years, researchers may be able to better characterize relationships between grass carp behavior and age.

Age-1 survival of triploid grass carp

The primary factor dictating triploid grass carp stocking numbers and frequency in an incremental stocking approach is the survival of fish in the infested system (Kirk and Socha 2003). Little is known about grass carp survival in most systems. Catch-curve analysis (Chapman and Robson 1960) has been used to analyze bowfishing-catch data (Morrow et al. 1997; Kirk et al. 2000), but only produces a single, point-estimate of average, annual mortality. While catch-curve analysis can be useful for characterizing trends in mortality over time, it does not reveal any information on how survival changes between ages. Classical mark-recapture methods could solve this problem, but grass carp are notoriously difficult to capture. Due to the many difficulties surrounding the capture of grass carp from large systems (Colle et al. 1978; Schramm and Jirka 1986; Chilton and Muoneke 1992; Bonar et al. 1993b), conventional mark-

recapture studies largely underestimate grass carp population size (Stott and Russell 1979). Since non-lethal methods for aging grass carp do not exist, the only live grass carp from which age can be reliably estimated are those marked at stocking or sterile fish that were stocked in a single event.

Methods have been developed to estimate survival of radio-tagged animals using mark-recapture models (Pollock et al. 1989; Pollock et al. 1995; Pine et al. 2003). These models have gained attention as useful tools in fisheries management (Hightower et al. 2001; Heupel and Simpendorfer 2002; Pollock et al. 2004; Waters et al. 2005; Thompson et al. 2007). These techniques have not been applied to estimate survival of grass carp. Furthermore, mark-recapture models can be useful for identifying factors that influence survival rates. Factors such as size of fish at stocking and stocking locations could potentially impact age-1 survival of grass carp. There are many factors controlled by management teams that could contribute to differences in grass carp survival. Information about changes in mortality due to such factors could be used to decrease cost or increase effectiveness of stocking grass carp.

Growth and mortality of grass carp

Knowledge of growth and mortality of grass carp can improve planning and assessment of weed-management plans that use the fish (Kirk and Socha 2003). Maximum ages and the growth rates of grass carp vary by geography, climate, availability of food resources, and age (Chilton and Muoneke 1992). Little research has been focused on defining growth rates of grass carp in natural systems. Most research on the growth of the species has occurred in aquaculture production systems (e.g., Kahn et al. 2004). Growth rates of grass carp, like many fish, are believed to be dependent on age (Sutton and Vandiver 1986; Chilton and Muoneke 1992). At

small sizes, growth rate is density dependent (Shelton et al. 1981). In grow-out operations, grass carp commonly reach lengths of 200 mm by 4 months (Thompson et al. 1987). Four years after stocking in Lake Wales FL, grass carp reached average lengths of 962 mm (Shireman et al. 1980). Average growth rates (mm) of fish were observed to decrease with age (Morrow et al. 1997), but that study only sampled fish up to 6 years of age and 15.6 kg. My preliminary findings indicate that the maximum age of grass carp in Lake Gaston is currently 16 years, and the maximum recorded weight is 34 kg. More research is needed to characterize age and growth of the older fish in this system.

In Lake Gaston volunteer bowfishers collect fish using methods similar to those used by Morrow et al. (1997). The catch of grass carp in Lake Gaston varies between sizes and ages of fish. Grass carp are collected throughout the year, and collection effort has never been measured or standardized. Because of the nature of grass carp collection, bowfishing data from Lake Gaston do not meet assumptions of equal catchability or constant effort required for catch-curve analysis. One alternative to estimating fish mortality with catch-based models is to model the mortality of grass carp using growth parameters. Growth parameters of grass carp can be estimated from length and age data (e.g., Rafail 1973), and they can be used to estimate average annual mortality of fish populations (Pauly 1980; Jensen 1996). Additionally, growth parameters can also be used to estimate age-specific mortality rates (Chen and Watanabe 1989). By approaching the question of grass carp mortality in Lake Gaston with several methods, overall understanding of mortality can be improved.

Study site

Lake Gaston (Figure 1.1) was formed in 1963 as a result of the construction of the Lake Gaston Dam by Virginia Electric and Power Company (VEPC) to control water level and generate electricity for Dominion Power (Pearsall et al. 2005). It is an impoundment of the Roanoke River, which flows from Southwest Virginia, through North Carolina into the Atlantic Ocean. The reservoir is 55 km long with over 560 km of shoreline, of which about 50% is undeveloped (Dominion Power 2005). The total surface area of Lake Gaston is 8,100 ha, with a total volume of about 5.6×10^{11} L flowing at $1,245 \text{ m}^3/\text{s}$, and a retention time of 29 days at full-pond elevation of 61 m (Dominion Power 2005; Richardson 2008).

Lake Gaston is bordered by the John H. Kerr Dam and Reservoir upstream, on the west end. Construction was completed on the Kerr Dam in 1953 by the US Army Corps of Engineers (USACE) as the primary flood-control station for the lower Roanoke River (Richter 1996; Pearsall et al. 2005). Kerr Reservoir is the primary input of water into Lake Gaston, and by comparison boasts a surface area of 19,500 ha. Roanoke Rapids Lake borders Gaston at the east (downstream) end, after which the Roanoke River flows unimpeded for 221 km to the Atlantic Ocean at Albemarle Sound (Carmichael et al. 1998). Some uses for water in Lake Gaston include recreational boating, fishing, and drinking water for residents of the city of Virginia Beach and the local Lake Gaston area (Cox 2007).

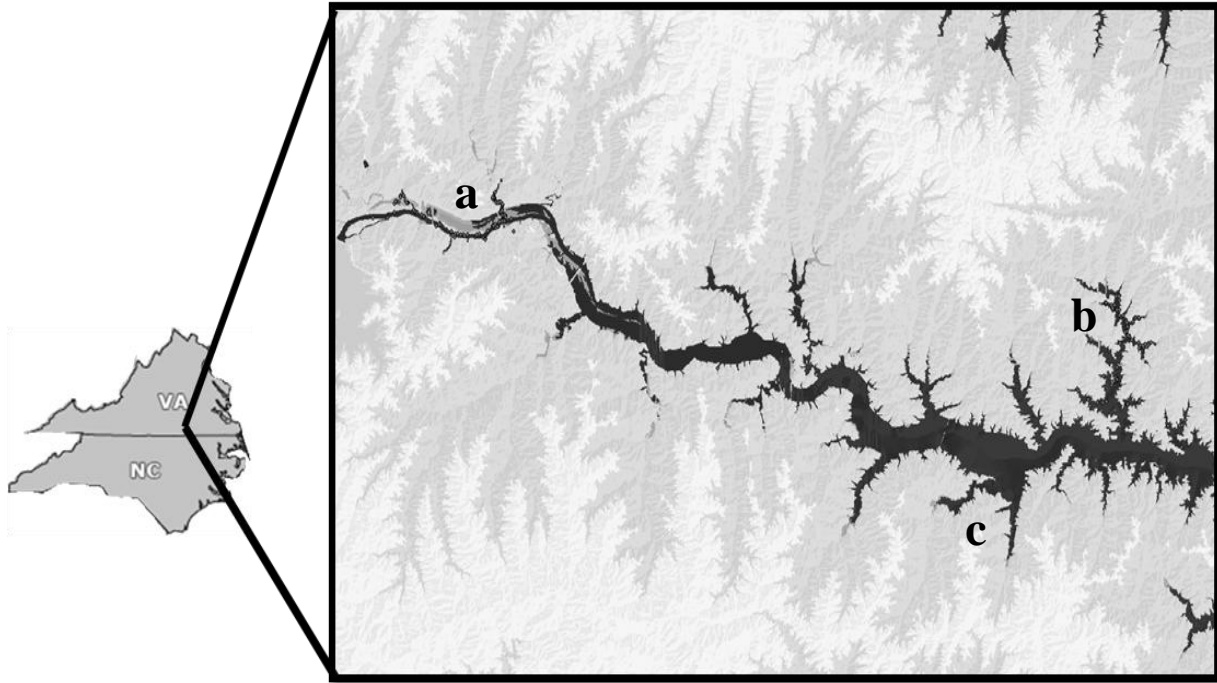


Figure 1.1.- Map of Lake Gaston with grass carp stocking locations used 2007-2009: (a) US-1 Boat Launch, (b) Pea Hill Creek, and (c) Big Stonehouse Creek. Stocking site (a) was the only site located in the upper reservoir. Stocked grass carp were divided between stocking sites (a) and (c) 2007-2008, and were divided between (a) and (b) in 2009.

Hydrilla was first identified in Lake Gaston in 1992 (Ryan et al 1995; Williams et al. 2008). Initial coverage in the lake was less than 10 ha (Williams et al. 2008). In Lake Gaston, incremental grass carp stocking is combined with low-level fluridone applications to control hydrilla (Williams et al. 2008). The Lake Gaston Weed Control Council (LGWCC) began stocking grass carp incrementally for hydrilla control in 1995. Low-level grass carp stockings (<20 fish/ha) have been combined with semi-annual herbicide applications to control hydrilla. Since 1995, about 80,000 triploid grass carp have been stocked into Lake Gaston (Table 1.1). Hydrilla coverage peaked at 1,364 ha in 2004 (Williams et al. 2008). In fall of 2010 hydrilla

coverage was about 666 ha (ReMetrix 2011). Important population parameters such as movement and distribution; post-stocking survival of grass carp; and the growth and mortality of grass carp are virtually unknown.

Table 1.1.- Stocking history of grass carp in Lake Gaston, Virginia and North Carolina, 1995-2010.

Year	# Stocked
1995	20,000
1997	680
1999	5,000
2003	25,392
2006	7,000
2007	7,720
2008	100
2009	6,520
2010	7,347

Study objectives

The goal of this study was to characterize the population ecology of grass carp used in an integrated weed management plan. The specific objectives of this study were to 1) determine movements and habitat use by grass carp in Lake Gaston, 2) estimate survival rates for age-1 grass carp in Lake Gaston, and 3) characterize growth, mortality, and population dynamics of grass carp in Lake Gaston. In order to achieve the above objectives I 1) used radio telemetry to monitor grass carp behavior, 2) estimated age-1 survival of grass carp in Lake Gaston, and 3) used age-and-growth data to estimate mortality and associated population parameters of grass carp.

Chapter 2: Movements and habitat use of grass carp in a large reservoir

Abstract: Grass carp *Ctenopharyngodon idella* have been stocked throughout the world and widely studied in the United States because of their potential as a biological control. In particular, grass carp have gained much attention due to their use in hydrilla *Hydrilla verticillata* control plans. In order to be an effective biological control, grass carp must remain in the system they were stocked in, and occupy areas targeted for weed control within those systems. One widely applied technique for understanding the behavior of grass carp is telemetry. While telemetry studies of grass carp are prominent in the literature, few studies have successfully identified mechanisms underlying behavioral changes. I used radio telemetry to monitor the movements and habitat use of 104 grass carp from 2007 to 2010 in a large, southeastern reservoir. Grass carp were followed for two years in Lake Gaston, North Carolina and Virginia, after release dates in 2007, 2008, and 2009. I characterized relationships between environmental factors and the movements and habitat use of grass carp. I found that grass carp occupied areas in the reservoir suitable for hydrilla growth through the first two years after tagging, and that emigration from Lake Gaston was unlikely. The average rate of movement for grass carp in Lake Gaston was about 137 m/d. Rapid dispersal after stocking was followed by long periods of no movement. However, when time after stocking was held constant in models of behavior, fish moved about 200 m/d more in the second year after stocking than in the first year, and were found closer to shore. On average, grass carp were found about 40 m from shore in about 2.5-3.5 m of water, although mean depth of water at grass carp locations varied seasonally, being shallowest in summer and deepest in winter. I found significant relationships between grass carp behavior and hydrological processes such as lake elevation and dam releases in the reservoir, as well as with other environmental factors such as water temperature, photoperiod, and weather.

For example, grass carp movement was positively correlated with changes in lake elevation. The results of this study provide useful information on the behavior of grass carp in a large, hydropower reservoir. I recommend that the primary use of reservoirs and the flow regimes of reservoirs be considered in grass carp-stocking risk assessments when the species is being considered for use in hydrilla-control plans. I also recommend that the relationships between grass carp behavior and flow dynamics should be studied further in future research. Finally, grass carp behavior appeared to differ between different ends of the reservoir with regard to how far they were located from shore. Since aspects grass carp behavior appears to differ between ends of Lake Gaston, I recommend that future research investigate other differences in grass carp ecology between the upper and lower reservoir. This knowledge could be useful for improving management decisions such as stocking locations in Lake Gaston and elsewhere.

Introduction

The grass carp *Ctenopharyngodon idella* has been studied throughout the world due to its utility as a biological control (Allen and Wattendorf 1987). When integrated with other weed-control methods, grass carp can provide a relatively inexpensive, long-term approach to aquatic weed control (Maceina et al. 1999; Chilton and Magnelia 2008). In systems with conflicting stakeholder opinions, an intermediate level of weed control can be a compromise between opposing viewpoints (Richardson 2008). Intermediate weed control is easiest to achieve in small water bodies (Cassani et al. 1995; Maceina et al 1999). As the size of a system increases, the effects of grass carp stocking rates become less predictable (Maceina et al. 1999). As a result stocking grass carp in large systems often results in complete eradication of all aquatic vegetation, or insufficient control of nuisance weeds (Stott and Robson 1970; Baker et al. 1974; Shireman and Maceina 1981; Kirk 1992; Bettoli et al. 1993; Schramm and Brice 1998).

One of the primary factors affecting the efficiency of noxious-weed control by grass carp in reservoir systems is movement to and from infested areas (Chilton and Poarch 1997). The most-effective control is achieved when grass carp remain in the system they are stocked in, and occupy areas targeted for weed control within that system (Nixon and Miller 1978). In their native range, grass carp can travel up to 500 km in their first two years of life (Gorbach and Krykhtin 1988). Prentice et al. (1998) observed one-way migrations of up to 325 km between several impoundments on the Guadalupe River in Texas. In the Mississippi River, movements by grass carp as great as 1,700 km have been documented (Guillory and Gasaway 1978). By 1986, diploid fish were found greater than 2,700 km from the initial stocking site in the Mississippi River after about 16 years in the river (Cudmore and Mandrak 2004). Due to its potential to make long-distance migrations, escapement from target areas is a major concern

related to stocking grass carp (Bain 1993; Maceina et al. 1999). If grass carp emigrate from a system or target areas within that system, there could be undesirable effects where the fish are unwanted (Clapp et al. 1993; Prentice et al. 1998).

There are several factors thought to affect grass carp movements and habitat use. One of the most important determinants in the magnitude of grass carp movements is believed to be life stage of the fish. The primary drivers of size or age at sexual maturity appear to be temperature and growth rate (Kahn et al. 2004). Long growing seasons and plentiful food supplies favor early maturation. In the Amur River, grass carp reach sexual maturity between 4 and 9 years at an average weight of 4.5 kg and lengths of 63-67 cm depending on latitude (Chilton and Muoneke 1993; Michewicz et al. 1972a). Bain et al. (1990) found that sexually mature grass carp (4.0-6.0 kg) moved greater distances than juveniles, and were not found in target areas as often. This behavior is similar to that described by Gorbach and Krykhtin (1988), where juveniles remained in downstream areas of rivers before migrating upstream as adults.

Studies on the effect of environmental factors on grass carp movements and distribution have yielded mixed results (Chilton and Muoneke 1993). Nixon and Miller (1978) found that grass carp activity was most limited by water temperature, but that day length and weather patterns had little effect on activity. Bain et al. (1990) showed that temperature and season had significant effects on the behavior of juvenile grass carp, but not adults. Cassani and Maloney (1991) found that neither water temperature nor day length had significant effects on grass carp movements; however, the range of temperatures available to grass carp was narrow (22.2-30.3°C), suggesting little seasonal fluctuation. The above range of temperatures is higher than the minimum temperature of 3-6 °C required for active grass carp feeding (Michewicz et al. 1972b), and less than the upper-lethal temperature of 38-39°C reported in the literature

(Opuszynski 1972; Bettoli et al. 1985). Grass carp movements might be affected more by a wider range of temperatures.

Water depth and column velocity occupied by grass carp are believed to be strongly associated with the presences of weed beds (Clapp et al. 1993). Grass carp usually are associated with shallow, near-shore environments (Mitzner 1978; Nixon and Miller 1978; Chilton and Muoneke 1993) where submersed vegetation is common. It is thought that high spring seasonal flows, in combination with temperature increases, may trigger spawning behavior in grass carp (Stanley et al. 1978). Studies have shown that grass carp generally occupy areas of relatively low flow rates (Beyers and Carlson 1993) but may avoid confined areas (Cassani and Maloney 1991). The effects of flow manipulation in hydro-power reservoirs on grass carp behavior are relatively unknown. It is possible that daily or seasonal fluctuations in flow regimes could impact grass carp movements and habitat use, and therefore the efficiency of noxious-weed control.

Despite the prominence of literature regarding grass carp movements and habitat use, few studies have successfully identified mechanisms behind changes in grass carp behavior. By understanding the mechanisms that affect movement and habitat use, researchers may be able to better understand factors that drive effective weed control by grass carp in large reservoirs. The objective of this study was to investigate relationships between environmental factors and movements and habitat use of grass carp used as a biological control for hydrilla *Hydrilla verticillata* in a large reservoir.

Methods

Study site

Lake Gaston (Figure 2.1) was formed in 1963 as a result of the construction of the Lake Gaston Dam to control water level and generate electricity for Dominion Power (Pearsall et al. 2005). Gaston is an impoundment of the Roanoke River, which flows from Southwest Virginia, through North Carolina into the Atlantic Ocean. The reservoir is 55-km long with over 563 km of shoreline, of which 50% is undeveloped (Dominion Power 2005). Gaston has a total surface area of 8,100 ha, a total volume of about 5.6×10^{11} L flowing at $1,245 \text{ m}^3/\text{s}$, and a retention time of 29 days at a full-pond elevation of 61 m (Dominion Power 2005; Richardson 2008).

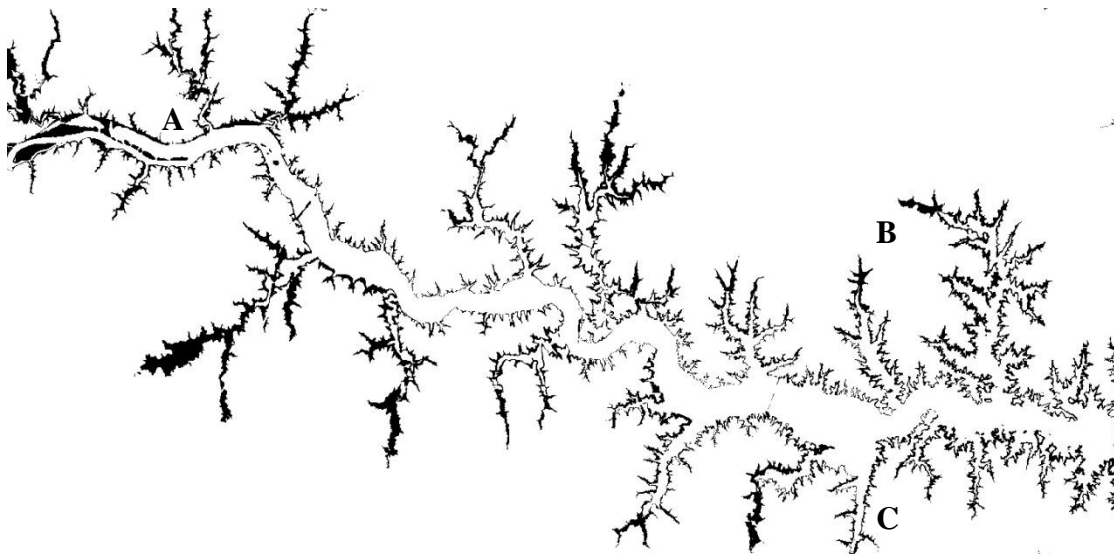


Figure 2.1.- Lake Gaston, North Carolina and Virginia. Grass carp stocking locations are shown as A) US Highway 1 public boat launch, B) Pea Hill Creek, and C) Big Stonehouse Creek. Stocking locations were grouped within the upper reservoir (A) and the lower reservoir (B and C) for behavioral analyses.

Radio-tagging methods and timeline

Grass carp have been stocked as part of a hydrilla-control plan in Lake Gaston since 1995. A total of about 80,000 fish were stocked from 1995-2010 (Table 2.1). From 2007 to 2009 grass carp were radio tagged at annual stocking events.

Table 2.1.- Stocking history of grass carp in Lake Gaston, VA and NC, 1995-2010.

Year	# Stocked
1995	20,000
1997	680
1999	5,000
2003	25,392
2006	7,000
2007	7,720
2008	100
2009	6,520
2010	7,347

Grass carp were tagged using conventional, internal-implant procedures and an experimental procedure for external attachment. Radio tags were surgically implanted in 61 fish in 2007 and 2008, and 15 fish in 2009. In 2009, some additional radio tags were externally attached (another 25 fish). In order to attach transmitters externally, attachment anchors (loops) were formed using 25-lb-test, monofilament line. The loops were attached to radio tags in a rectangle about a single plane of the tag with epoxy. The epoxy was allowed to set for 24 hours.

A total of 101 radio-tagged grass carp were stocked into Lake Gaston from 2007 to 2009 (Table 2.2). Model F1820 radio tags with trailing-whip antennae from Advanced Telemetry Systems (ATS, Inc., Isanti, MN) were used for all radio-tagged grass carp from 2007 through spring 2009. Radio tags weighed 8-25 g, and had an expected battery life of 536 d. Tag frequencies ranged from 150.000 to 151.999 MHz.

Table 2.2.- Tagging information for radio-tagged grass carp released in Lake Gaston 2007-2009.

Release date	No. tagged internally	No. tagged externally	Mean fish weight (g)	Mean fish length (mm, TL)
16 May 2007	29	0	-	333
26 May 2008	32	0	535	368
20 April 2009	15	25	1111	467

Internal implant surgery.- Fish were anesthetized with MS-222 in a holding tank prior to all surgeries. Surgical tools were disinfected in a 10-ppt iodine solution. After anesthetizing, fish were placed ventral side up in a v-shaped saddle. Water pumps were used to circulate anesthetic through the fish's gills throughout the procedure. A small (2-cm) incision was made, offset slightly from the ventral line of the fish. A transmitter was gently inserted through the incision. The incision was closed with three to four knots using non-absorbable, monofilament sutures. Fish were observed to recover before being released into the lake. Maximum time for implant surgery (including anesthetization and recovery) was about 15 minutes.

External attachment procedure.- Grass carp were prepared for transmitter attachment following methods described above, but were placed ventral-side down in the surgery saddle. A rear-attachment wire (16-gauge sterilized surgical steel) was passed through the dorsal musculature, below the spine, using a curved taxidermy needle, and was then passed through two loops on either side of the radio tag. The radio tag was then tightened by twisting the attachment wire 7 to 8 times above the tag. The same procedure was repeated about 3-cm anterior to the initial insertion. After the forward-attachment wire was tightened, the forward- and rear-attachment wires were twisted together 8 to 10 times. The wires were trimmed and folded flat

against the dorsal surface of the radio tag pointing backward. Fish recovered before being released into the lake. Maximum time for attachment (including anesthetization and recovery) was 10 minutes.

Collection and analysis of telemetry data

Radio-tagged grass carp were divided and released at public boat launches at US 1 in Virginia and Salmon's landing in North Carolina (see Figure 1) during 2007 and 2008. In 2009, fish were divided and released at US 1 and Pea Hill Creek in Virginia. Grass carp were radio tracked using boat-mounted Yagi antennae from 2007 through 2010. In 2007, an aerial survey was conducted to assess escapement of grass carp from Lake Gaston. The aerial survey did not show any evidence that radio-tagged grass carp had escaped from Lake Gaston. Over 800 individual locations of live fish were logged by manually tracking from a boat. Once a fish was located, its position (UTM, NAD83) was recorded using a hand-held Garmin GPSmap76CSx (Garmin International Inc., Olathe, Kansas). The unit was a recreational-grade GPS with an accuracy of ± 5 m. Date, time, secchi depth, water depth, surface temperature, and distance to the nearest shoreline were measured at each fish location. Average daily wind speed was noted for each tracking day. I used hydrology data (inflow to the lake, outflow from the lake, lake elevation, and rainfall) from the United States Army Corps of Engineers (USACE) hydrologic monitoring station at the John H. Kerr Dam. I estimated daily hours of daylight using sunrise and sunset times in Raleigh, NC (~120 km SE of Gaston) for each sample day.

I calculated average daily movement (ADM) of grass carp as the Euclidean distance traveled (UTM, m) between consecutive fish locations, divided by the number of days elapsed between sampling events. Average daily movement is an index of activity that allows for

movement rate to be standardized by a common unit of time. Movement indices such as ADM are often used to investigate seasonal and annual trends in movement (e.g., Chilton and Poarch 1997; Frost et al. 2009).

Univariate analyses.- Due to constraints of data structure, I used univariate methods to test the effects of categorical variables on movements and habitat use of grass carp. To account for random variation between fish, ADM, depth, and distance to shore were averaged across individual fish prior to analysis. The grand mean for each response variable in univariate tests was a weighted mean based on the number of times each fish was located. I tested the effects of season on the depth of water occupied by grass carp (m) and the distance of grass carp to the nearest shoreline (m) using one-way analysis of variance (ANOVA) (Zar 1999). I did not test the effects of season on movement because of known relationships between movement of grass carp and the amount of time elapsed after stocking (Chilton and Poarch 1997). I used Tukey-Kramer pair-wise comparisons of means to determine differences in habitat use (water depth and distance to shore) between seasons (spring, summer, fall, winter) (Zar 1999). I used two-sample t-tests to determine differences in ADM, depth, and distance to shore due to stocking location and to test for differences between movements due to tagging method (Zar 1999). Statistical significance was inferred at $p \leq 0.05$ for all tests.

Multiple-regression analyses.- I used multiple-linear regression (MLR) to characterize the relations between several abiotic factors and grass carp movements (ADM) and habitat use (depth and distance to shore). I fit all possible regression models of each response variable using several predictor variables, including: age (yr), water temperature ($^{\circ}\text{C}$), secchi depth (m), days

post-tag (d), days elapsed (d), elevation (m), inflow (m³/s), outflow (m³/s), rain (mm), wind speed (km/h), and hours of daylight (h). For analysis of movements (ADM), response data were transformed as $\log_e(\text{ADM}+1)$ to normalize distribution (Rogers and White 2007). The distance of grass carp from the nearest shoreline was also \log_e -transformed to achieve a normal distribution in the response. Water depth at grass carp locations was not transformed for analysis.

I used global F -tests to determine whether any of the response variables were related to any of the predictors in each multiple linear regression model (Montgomery et al. 2006). I used individual t -tests to determine the significance of relationships between each response variable and each predictor (Montgomery et al. 2006). Since a considerable amount of colinearity was present in the fully parameterized models of ADM, depth, and distance to shore, I selected the 5 best models of each response from all possible subsets to discuss. For construction of ADM models, age, temperature, days post-tag, days elapsed after tagging, lake elevation, rain, and wind speed were included in all models due to correlations between these predictors and ADM. Similarly, fish age, water temperature, and wind speed were all included in each model of depth. Water temperature, secchi depth, lake elevation, wind speed, and hours of daylight were each included in all models of grass carp distance from the nearest shoreline. I characterized relationships between predictors using simple linear regression. I determined the presence of colinearity between predictors in all models using variance inflation factors (VIFs), using VIFs of 10 or more as indicators of substantial colinearity (Montgomery et al. 2006). I ranked the five-best models of each response variable based on R^2 -adjusted, the $PRESS$ statistic, and Mallows' C_p model-fit statistics (Montgomery et al. 2006).

Results

A total of 11, 9, and 9 predictors were used to model ADM, depth, and distance to shore, respectively (Table 2.3). Preliminary analyses indicated a high degree of correlation between predictors used in this study (Table 2.4). Therefore, I report partial coefficients of determination, and VIFs for each predictor used in the five best models of each response.

Table 2.3.- Mean values and standard deviations (SD) of predictors used in multiple regression analyses. Predictors used in modeling each response are indicated by *y*.

Predictor	Mean	SD	Used in models (y/n)		
			ADM (m)	Depth (m)	Shore (m)
Age (yr)	1.3	0.35	<i>y</i>	<i>y</i>	<i>y</i>
Water Temperature (°C)	20	8.0	<i>y</i>	<i>y</i>	<i>y</i>
Secchi Depth (m)	1.0	4.4	<i>y</i>	<i>y</i>	<i>y</i>
Days Post-tag (d)	174	149	<i>y</i>	<i>n</i>	<i>n</i>
Days Elapsed (d)	43	59	<i>y</i>	<i>n</i>	<i>n</i>
Elevation (m)	61	0.08	<i>y</i>	<i>y</i>	<i>y</i>
Inflow (m ³ /s)	223	194	<i>y</i>	<i>y</i>	<i>y</i>
Outflow (m ³ /s)	194	188	<i>y</i>	<i>y</i>	<i>y</i>
Rain (mm)	2	5	<i>y</i>	<i>y</i>	<i>y</i>
Wind speed (km/h)	5	4	<i>y</i>	<i>y</i>	<i>y</i>
Hours of Daylight (h)	13	1.8	<i>y</i>	<i>y</i>	<i>y</i>

Table 2.4.- Correlation matrix showing Pearson correlation coefficients (r) for relationships between predictors used in multiple regression analyses. *Indicates statistically significant relationships.

	Age (yr)	Water Temp. (°C)	Secchi Depth (m)	Days Post- tag	Days Elapsed	Elevation (m)	Inflow (m ³ /s)	Outflow (m ³ /s)	Rain (mm)	Wind speed (km/h)	Hours of Daylight
Age (yr)	1	-0.05	-0.02	0.79*	0.55*	-0.06	-0.20*	-0.14*	0.16*	0.06	0.08*
Water Temp. (°C)		1	0.04	-0.54*	-0.25*	-0.33*	-0.53*	-0.53*	-0.01	-0.32*	0.78*
Secchi Depth (m)			1	-0.04	-0.02	0.01	-0.02	-0.04	0.05	-0.01	0.05
Days Post-tag (d)				1	0.58*	0.03	-0.03	0.08*	0.14*	0.27*	-0.42*
Days Elapsed (d)					1	-0.10*	-0.09*	-0.04	0.00	0.06	-0.08*
Elevation (m)						1	0.29*	0.24*	-0.05	0.12*	-0.20*
Inflow (m ³ /s)							1	0.92*	-0.12*	0.15*	-0.34*
Outflow (m ³ /s)								1	-0.08*	0.17*	-0.47*
Rain (mm)									1	0.13*	0.07*
Wind speed (km/h)										1	-0.32*
Hours of Daylight											1

Movements of grass carp

Univariate analyses.- Mean ADM of grass carp (\pm SE) was about 137 m/d (\pm 26 m/d).

Grass carp ADM did not differ significantly between fish tagged internally or externally ($df=1$, $t=-1.32$, $p=0.206$) or between fish stocked at different locations ($df= 1$, $t=1.09$, $p=0.2752$).

Multiple regression analyses.- Relationships between ADM and predictors used in regression analysis are shown in Figure 2.2. The five best regression models of grass carp ADM all included water temperature, fish age, number of days post-tag, number of days elapsed between consecutive telemetry locations, lake elevation, rainfall, and wind speed (Table 2.5). A moderate degree of colinearity ($VIF > 5$) existed only in Model M4. Colinearity, as indicated by

VIFs, was lowest in models M1 and M2. These models were similar to one another, and both provided reasonable fits to the data. The primary difference between models M1 and M2 was that model M1 included inflow and M2 included outflow. Movement appeared to best represented within this model set by models that contained all variables that were significantly related to ADM in addition to a single index of flow. Such models were nearly indistinguishable in terms of performance as measured by model-fit statistics, suggesting that either model M1 or M2 provide a reasonable representation of fish movement.

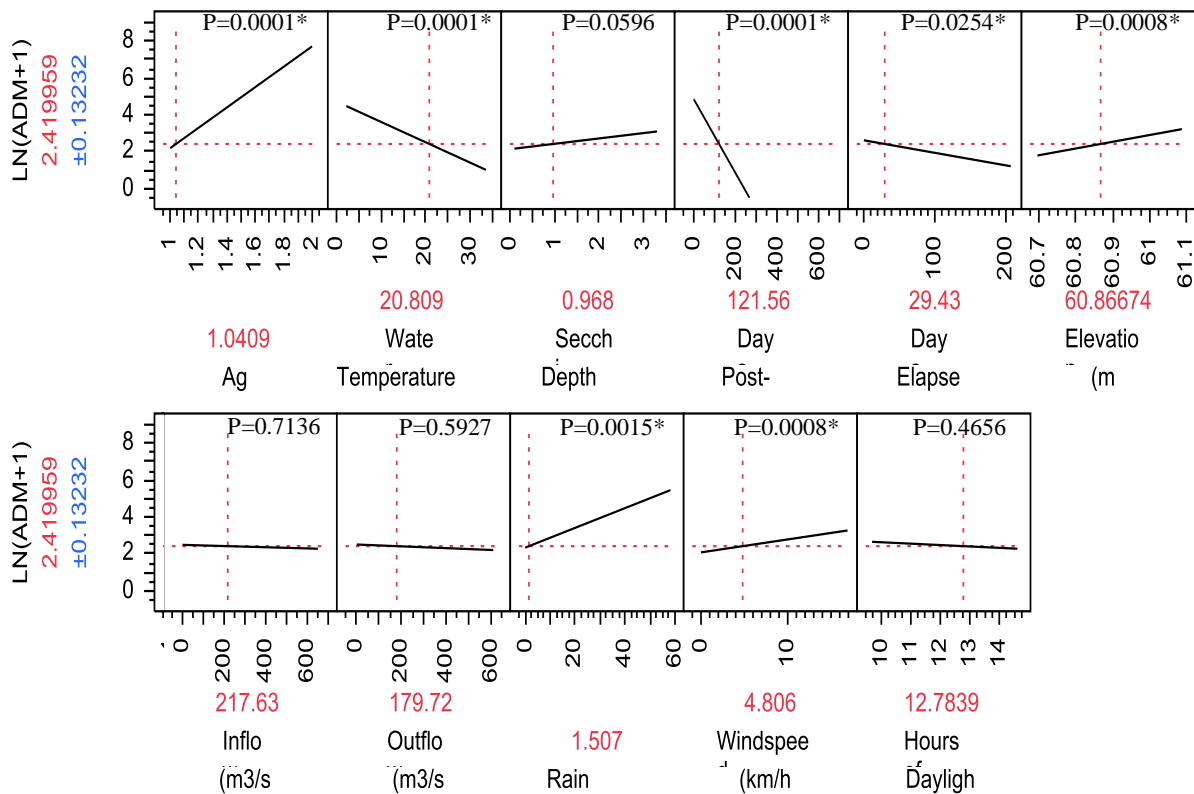


Figure 2.2.- Graphical correlation matrix describing relationships between predictors and ADM. Mean values for each variable are given in red. Standard error of the response (ln-transformed) is given in blue. *indicates statistically significant correlations.

Table 2.5.- Predictors used and model-fit statistics for the five-best candidate models of ADM. P is the number of parameters estimated, C_p is the value of Mallows' C_p statistic for each model, R^2_{ADJ} is the R^2 -adjusted value for each model, and $PRESS$ is the value of the $PRESS$ statistic. Partial coefficients of determination (r^2) and variance inflation factors (VIFs) are given for all predictors used in each model.

Predictor	M1		M2		M3		M4		M5	
	r^2	VIF	r^2	VIF	r^2	VIF	r^2	VIF	r^2	VIF
Age (yr)	0.12	1.81	0.11	1.83	0.11	2.04	0.07	3.14	0.11	2.04
Water Temperature (°C)	0.12	2.18	0.19	2.04	0.10	1.57	0.18	3.05	0.10	1.76
Secchi Depth (m)					0.02	1.01			0.03	1.01
Days Post-tag (d)	0.34	3.04	0.32	3.04	0.27	3.2	0.14	6.83	0.28	3.22
Days Elapsed (d)	0.00	1.42	0.00	1.41	0.01	1.46	0.00	1.41	0.00	1.48
Elevation (m)	0.00	1.2	0.00	1.18	0.01	1.07	0.00	1.19	0.01	1.07
Inflow (m ³ /s)	0.01	1.47								
Outflow (m ³ /s)			0.01	1.46			0.01	1.46	0.00	1.26
Rain (mm)	0.01	1.13	0.00	1.13	0.01	1.11	0.01	1.22	0.01	1.12
Wind speed (km/h)	0.01	1.27	0.01	1.27	0.01	1.29	0.01	1.27	0.00	1.32
Hours of Daylight (h)							0.00	6.73		
P	8		8		9		9		9	
C_p	2.3		3.5		2.5		3.7		3.9	
R^2 -Adj	47.3		47.4		44.6		47.4		44.5	
$PRESS$	1671		1665		1672		1672		1463	

Of the predictors measured in this study, water temperature, the age of fish, number of days post-tag, and wind speed were most strongly related to grass carp movement (Table 2.6). Movement decreased with increased time after stocking, but when all other factors were held

constant, a 1-year increase in grass carp age corresponded to an increase in ADM of about 200 m/d in ADM. Lake elevation was also correlated with grass carp ADM. A 1-meter increase in lake elevation corresponded to an increase of about 7 m/d in grass carp ADM when other factors were held constant. Grass carp moved more when rain or wind speed increased and other factors were held constant. Grass carp ADM was less when water temperature, number of days between telemetry locations, or inflow were increased, given all other factors held constant.

Table 2.6.- Standardized coefficients (β_i) and individual statistics for parameters estimated in one of the best models of grass carp ADM in Lake Gaston (model M1).

Predictor	β_i	t	p
Fish age (yr)	-0.44043	12.44	0.000
Water Temperature (°C)	-1.39203	-10.71	0.000
Days post-tag (d)	-0.10053	-20.74	0.000
Days elapsed (d)	0.06962	-1.37	0.172
Lake elevation (m)	-0.00009	2.26	0.024
Inflow (m ³ /s)	0.13229	-3.33	0.001
Rain (mm)	0.11779	3.51	0.000
Wind speed (km/h)	0.73379	3.54	0.000

Depth of water at grass carp locations

Univariate analyses.- Grass carp were found in shallow water in Lake Gaston at a mean depth (\pm SE) of about 2.9 m (\pm 0.08 m). Depth of water at grass carp locations varied significantly by season (Figure 2.3) ($df=3$, $F=4.495$, $p=0.0042$). Grass carp were found in the

deepest water during winter and the shallowest water during summer. Water depth at grass carp locations was not significantly different between the upper and lower reservoirs ($df=1$, $t=0.239$, $p=0.8117$).

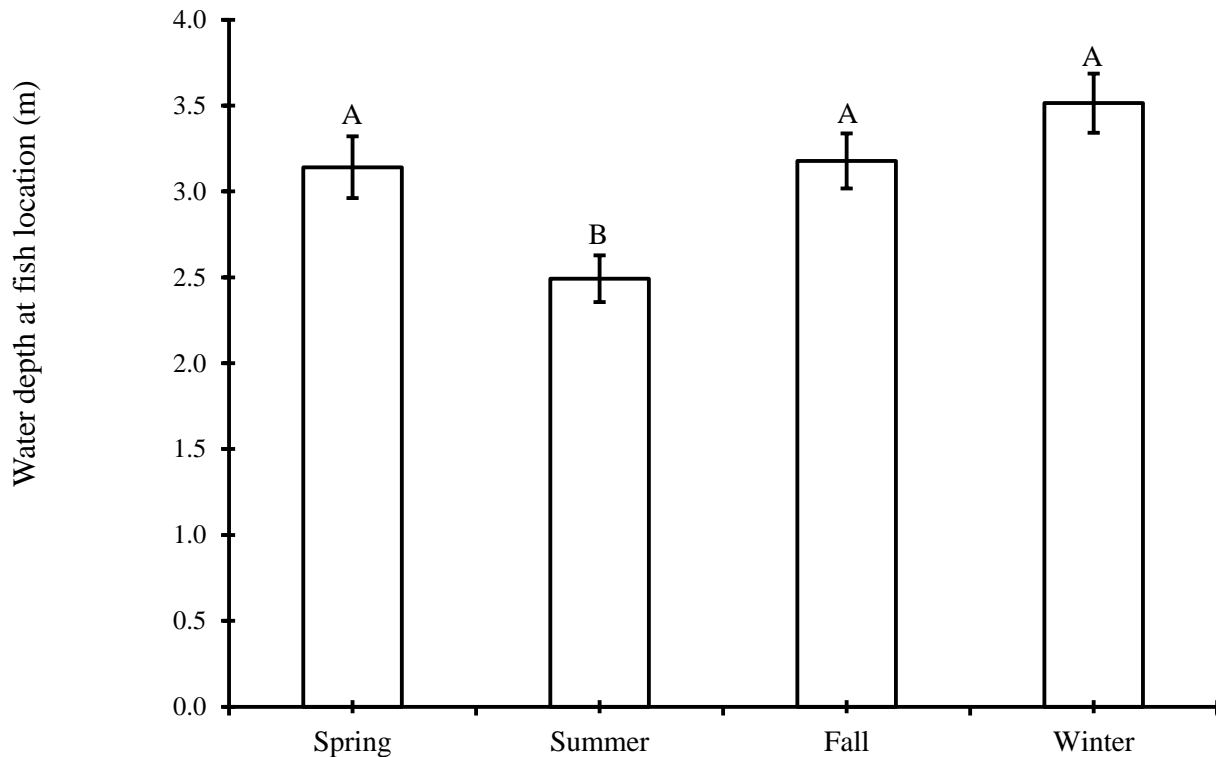


Figure 2.3.- Average seasonal water depth at grass carp locations (\pm SE) in Lake Gaston.

Multiple regression analyses.- Significant relationships were observed between water depth at grass carp locations and predictors (Figure 2.4). All five of the best regression models of water depth at grass carp locations included fish age, water temperature, and wind speed (Table 2.7). None of the best models included secchi depth. Model D1 provided the best representation of water depth at grass carp locations because it had the smallest value for Mallows' C_p , the smallest *PRESS* statistic, and the smallest VIFs of any model.

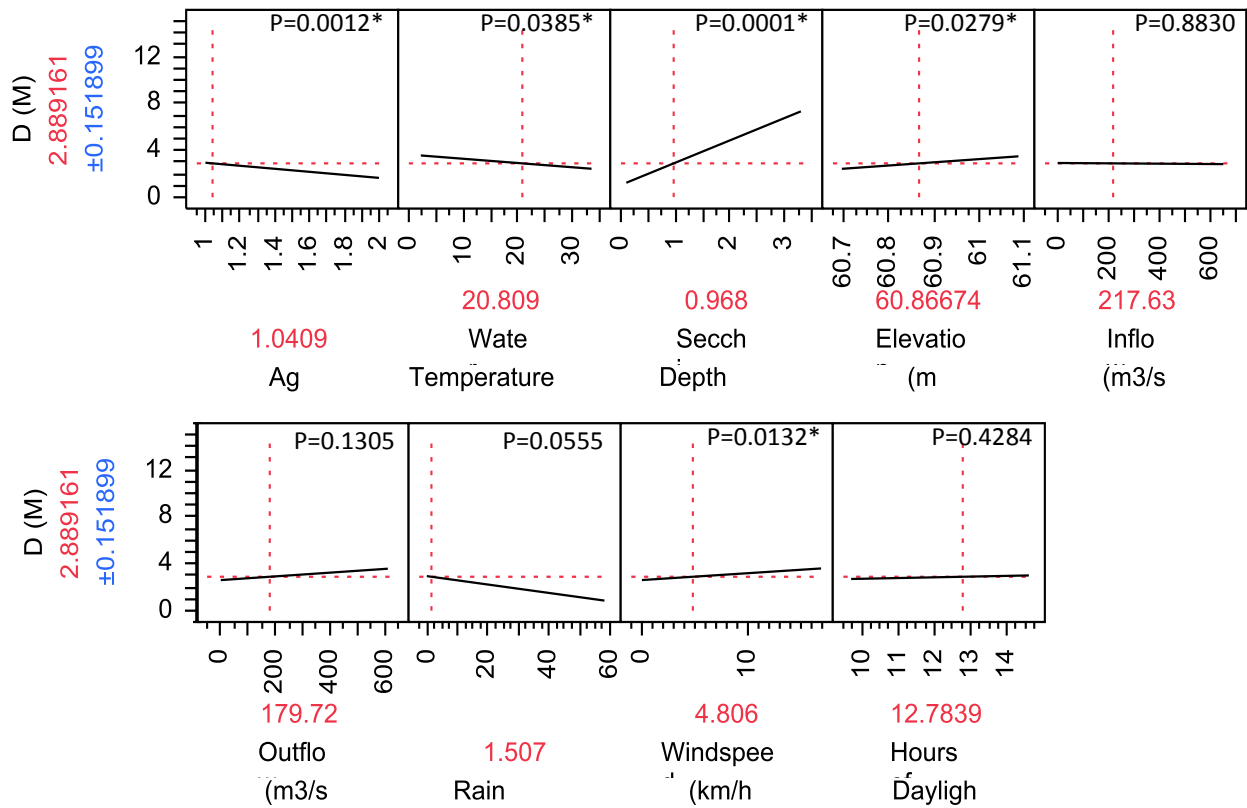


Figure 2.4.- Graphical correlation matrix of water depth at grass carp locations [D(M)] and individual predictors used in multiple regression analysis. Mean values for each variable are given in red. Standard error of the response is given in blue. *Indicates statistically significant correlations.

Table 2.7.- Predictors used and model-fit statistics for the five-best candidate models of water depth at fish location. P is the number of parameters estimated, C_p is the value of Mallows' C_p statistic for each model, R^2_{ADJ} is the R^2 -adjusted value for each model, and $PRESS$ is the value of the $PRESS$ statistic. Partial coefficients of determination (r^2) and variance inflation factors (VIFs) are given for all predictors used in each model.

Predictor	D1		D2		D3		D4		D5	
	r^2	VIF	r^2	VIF	r^2	VIF	r^2	VIF	r^2	VIF
Age (yr)	0.02	1.01	0.02	1.01	0.02	1.01	0.02	1.01	0.02	1.01
Water Temp. (°C)	0.04	1.47	0.04	1.12	0.04	1.47	0.04	1.54	0.04	1.46
Secchi Depth (m)										
Elevation (m)							0.00	1.14		
Inflow (m ³ /s)									0.01	1.43
Outflow (m ³ /s)	0.01	1.409			0.01	1.1	0.01	1.42		
Rain (mm)			0.01	1.08	0.00	1.21			0.00	1.11
Wind speed (km/h)	0.01	1.122	0.01	1.19	0.01	1.43	0.01	1.13	0.01	1.21
Hours of Daylight (h)										
P	4		4		5		5		5	
C_p	2.3		3.5		2.5		3.7		3.9	
R^2_{ADJ}	8.8		8.6		9		8.9		9	
$PRESS$	2721		2722		2724		2730		2725	

Water temperature was the strongest predictor of water depth at grass carp locations (Table 2.8). Grass carp generally were found in shallower water when water temperatures were high. A 1-year increase in age corresponded to a 1.6-m decrease in the average depth occupied

by grass carp when all other factors were held constant. Water depth occupied by grass carp increased with outflow when other factors were held constant and on windy days if other factors were held constant.

Table 2.8.- Standardized coefficients (β_i) and individual statistics for parameters estimated in the best model of water depth at grass carp locations in Lake Gaston (model D1).

Predictor	β_i	T	p
Fish Age (yrs)	-0.22323	-3.920	0.000
Water Temperature (°C)	-3.08498	-3.790	0.000
Outflow (m ³ /s)	0.00007	2.140	0.033
Wind Speed (km/h)	0.07295	1.800	0.073

Distance of grass carp from the nearest shoreline

Univariate analyses. - Grass carp were located a mean distance of 40 m from the nearest shore (± 1.9 m) throughout the year in Lake Gaston. The distance of grass carp to the nearest shoreline did not appear to vary by season ($df=3$, $F=2.22$, $p=0.0861$), however grass carp stocked in the upper reservoir were located closer to shore than grass carp stocked in the lower reservoir ($df=1$, $t=-2.028$, $p=0.0456$) (Figure 2.5).

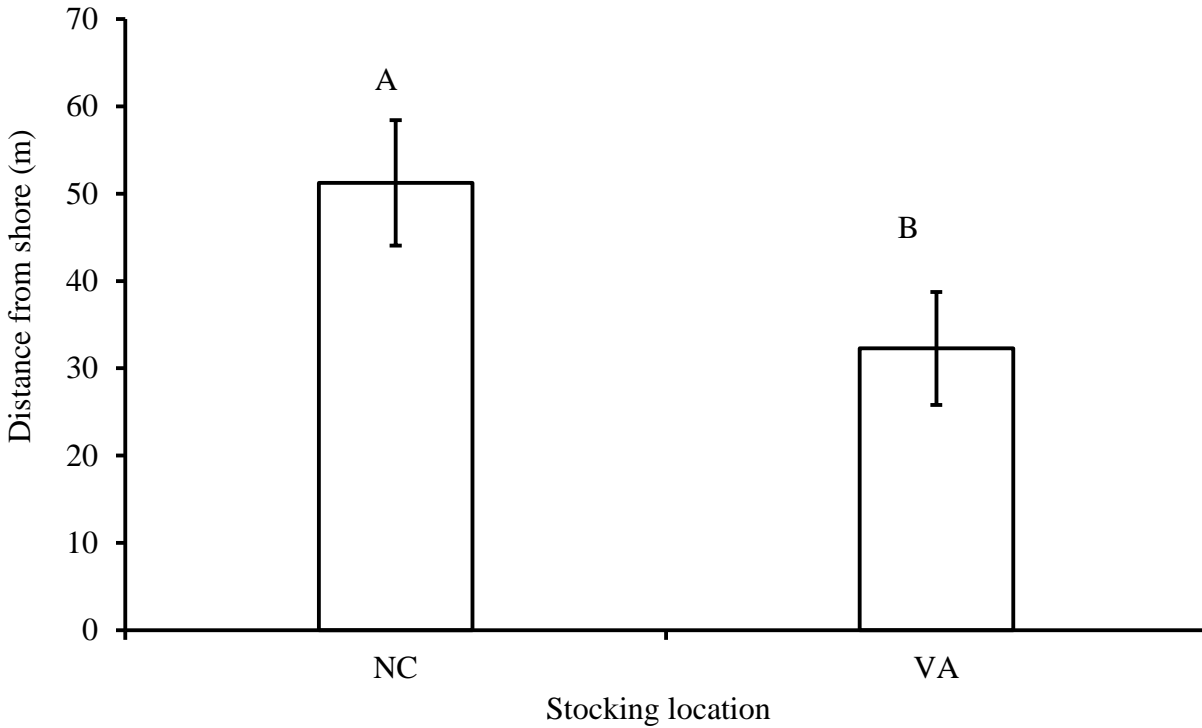


Figure 2.5.- Mean distance of grass carp to the nearest shoreline (\pm SE) in Lake Gaston by stocking location.

Multiple regression analyses.- All five of the best models of grass carp distance from the nearest shoreline included water temperature, secchi depth, lake elevation, wind speed, and hours of daylight (Table 2.9). Significant correlations were observed between grass carp distance to shore and predictors (Figure 2.6). Model S1 was the best model developed to explain the distance of grass carp to the nearest shoreline according to model-fit statistics. Model S1 had the largest R^2_{ADJ} value and the smallest values for Mallows' C_p and $PRESS$ statistics.

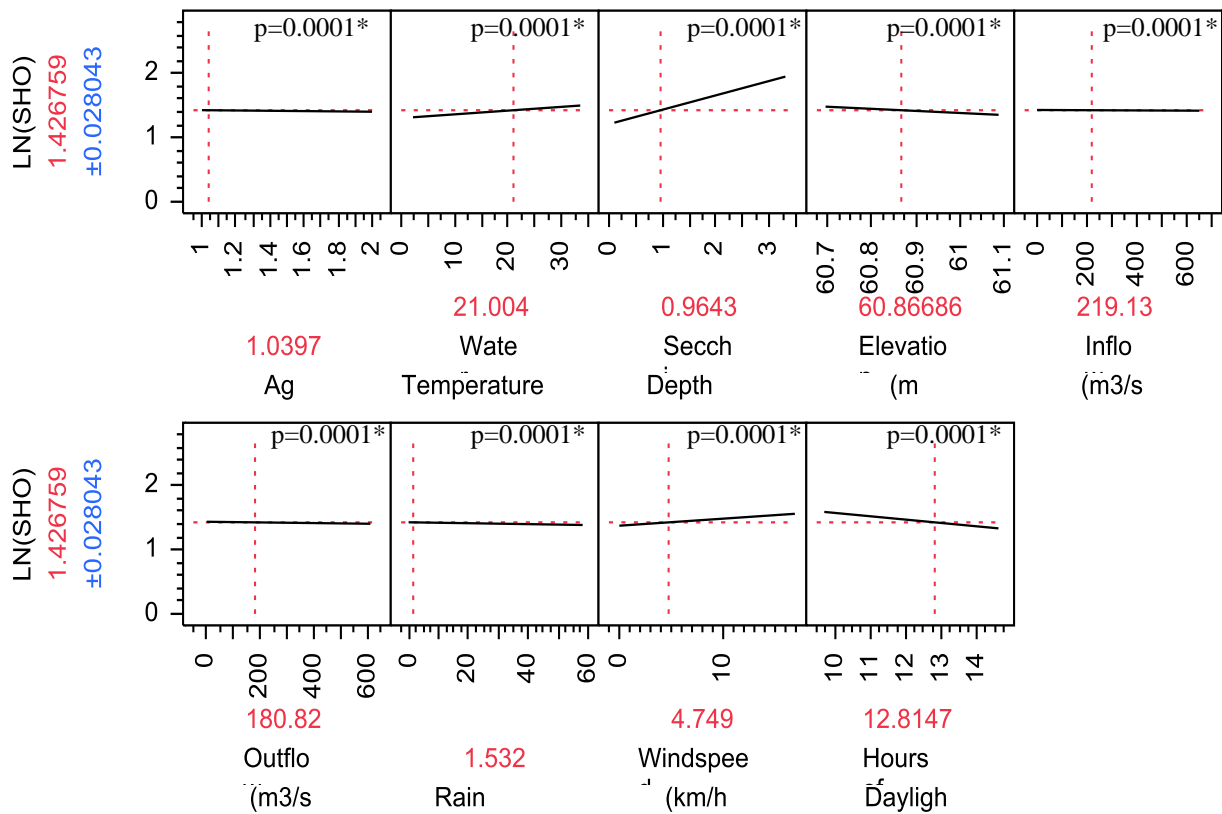


Figure 2.6.- Graphical correlation matrix of relations between distance of grass carp to the nearest shoreline [LN(SHO)] and predictors. Mean values for each variable are given in red. Standard error of the response (ln-transformed) is given in blue. *indicates statistically significant correlations.

Table 2.9.- Predictors used for modeling distance of grass carp from the nearest shoreline. P is the number of parameters estimated, C_p is the value of Mallows' C_p statistic for each model, R^2_{ADJ} is the R^2 -adjusted value for each model, and $PRESS$ is the value of the $PRESS$ statistic. The partial coefficient of determination (r^2) and variance inflation factors (VIFs) are given for all predictors used in each model.

Predictor	S1		S2		S3		S4		S5	
	r^2	VIF	r^2	VIF	r^2	VIF	r^2	VIF	r^2	VIF
Age (yr)					0.01	1.02				
Water Temperature (°C)	0.01	2.31	0.01	2.52	0.00	2.33	0.01	2.74	0.01	2.36
Secchi Depth (m)	0.02	1.00	0.04	1.00	0.01	1.00	0.00	1.00	0.02	1.01
Elevation (m)	0.01	1.06	0.03	1.06	0.00	1.06	0.01	1.06	0.01	1.06
Inflow (m ³ /s)							0.00	1.31		
Outflow (m ³ /s)			0.02	1.19						
Rain (mm)									0.00	1.14
Wind speed (km/h)	0.01	1.16	0.03	2.21	0.01	1.16	0.01	1.17	0.01	1.26
Hours of Daylight (h)	0.04	2.21	0.06	1.27	0.03	2.21	0.03	2.27	0.03	2.33
P	5		6		6		6		6	
C_p	3.2		4.6		4.7		4.7		5.2	
R^2_{ADJ}	6		5.9		5.9		5.9		5.8	
$PRESS$	360		361		362		361		362	

Water temperature was most strongly related to grass carp distance from shore when all other factors were held constant (Table 2.10). Grass carp were found significantly further from shore when water temperature was high if all other factors were held constant. Increases in water transparency (secchi depth) and average daily wind speed also corresponded to increases

in the distance of grass carp to the nearest shoreline when other factors were constant. When pool elevation was high, grass carp were found closer to shore. Grass carp were found closer to shore when there were fewer hours of daylight and other factors were held constant.

Table 2.10.- Standardized coefficients (β_i) and individual statistics for the best model of grass carp distance from the nearest shoreline (model S1).

Predictor	β_i	T	p
Water Temperature (°C)	0.042	2.030	0.043
Secchi Depth (m)	0.001	2.010	0.045
Elevation (m)	-0.002	-2.370	0.018
Wind speed (km/h)	0.002	2.230	0.026
Hours of Daylight (hr)	-0.011	-4.560	0.000

Discussion

Grass carp behavior in Lake Gaston appeared to be most strongly associated with age and the amount of time a fish was in the lake. Grass carp movement rates decreased rapidly after release as observed by Bain et al. (1990) and Chilton and Poarch (1997). After an initial dispersal period, grass carp were found most often in small creeks and backwaters near stocking areas, and moved little until their second spring season. However, when the number of days post-tag was held constant, grass carp movement increased with age. At age 2, all fish moved out of small creeks and were frequently found throughout the main lake. This behavior is similar to that described by Gorbach and Krykhtin (1988) who suggested that juvenile grass carp may spend several years in rearing habitats before adapting behavioral characteristics of adults, and

Cassani and Maloney (1991) who suggested that juvenile, post-stocking home ranges of grass carp may last from three months to one year. Age-2 fish were found in shallower water depths than age-1 fish, and grass carp were not found any further from shore than at age one. My findings are contrary to those of Bain et al. (1990) who speculated that as grass carp aged, they would move away from areas suitable for hydrilla growth. One possible reason for this is that I followed the same fish for multiple years in Lake Gaston. Bain et al. (1990) followed different fish in each year. Thus, it is possible that the results of their study indicate differences in post-stocking behaviors between juvenile and adult grass carp rather than differences in life-history strategies at different ages. The behaviors exhibited by grass carp in Lake Gaston suggest that movements and habitat use of the fish may change with age, but fish continue to occupy areas within the range of depth occupied by hydrilla.

By holding constant the relationship between days post-tag and ADM, I was able to examine relationships between movement and seasonal factors individually. Chilton and Poarch (1997) reported that the interpretation of trends in seasonal movements was confounded by a rapid decrease in movement after stocking. Results reported by Bain et al. (1990) also suggested that seasonal trends in movement may have been related to time after stocking, but time after stocking was not accounted for in that study. While my methods do not provide a direct means of testing the effect of season on movement, I was able to determine the influences of individual factors that might be included in delineation of seasons. Such factors included water temperature and hours of daylight. The results of my study indicate the interactions between seasonal factors and grass carp behavior may be more complex than has previously been assumed. For example, previous studies have found that grass carp activity was lowest in winter (Nixon and Miller 1978; Bain et al. 1990; Chilton and Poarch 1997). However, grass carp may feed in water

temperatures as low as 3-6°C (Michewicz et al. 1972b). My results suggest that grass carp move the least when water temperature is high and all other factors are held constant. One possible explanation for this phenomenon is that the high summer temperatures in Lake Gaston may cause the fish to move less. Researchers have speculated that grass carp are adapted to conserve energy at high temperatures (Huisman and Valentijn 1981). Furthermore, dissolved oxygen (O₂) may be more limiting to juvenile grass carp survival in summer months than in winter months (Opuzynski 1967). If O₂ is limiting to survival, then minimizing movement during warm months may be a useful strategy for maintaining low metabolism and, therefore, O₂ consumption rates. However, Nixon and Miller (1978) found no effect of O₂ on movement. As an alternative explanation, grass carp may move less when temperatures are high because that is when hydrilla growth peaks. Previous research suggests that grass carp graze most efficiently when they move the least (Hockin et al. 1989) and that grass carp move little after locating vegetation (Chilton and Muoneke 1992; Chilton and Poarch 1997). It is possible that the lack of movement observed at high temperatures in Lake Gaston indicates periods of heaviest grazing by grass carp on hydrilla. This speculation is supported by the observation that grass carp were found in the shallowest water during summer, where food is presumably more plentiful (Chilton and Muoneke 1992). Although I observed no effect of season on the distance of grass carp to the nearest shoreline, I did find that grass carp were located closer to shore during periods of extended daylight.

Another possible explanation for my observation that ADM increased with decreasing temperature is that temperature may not be the most-important seasonal influence on grass carp ADM. If temperature was a reliable predictor of seasonality in grass carp movements, I also would expect that photoperiod (hours of daylight) would be a significant predictor of fish

activity. However, photoperiod was only included in the worst model of grass carp ADM, suggesting that water temperature may be a statistically more-useful index of season than photoperiod for ADM; possibly because cues based on photoperiod are less relevant in this sterile population, temperature was quantified more accurately, or because temperature varied more in this study. A similar result was observed in the distance of grass carp to the nearest shoreline. The relationship between shoreline orientation and temperature suggested opposite behavioral patterns than did the relationship between shoreline orientation and photoperiod. These results suggest that seasonal conditions may not be as important in influencing grass carp movements as conditions that change day to day, such as weather patterns and flow dynamics. The only response variable measured in this study that appeared to be clearly dependent upon temperature (according to both univariate and MLR analyses) was depth of water at fish locations, and photoperiod was not included in any of the best models of depth. As described in other studies (Nixon and Miller 1978; Bain et al. 1990), I found that grass carp were found in deeper water during winter months. Similarly, the multiple-regression analysis showed that grass carp were found in deeper water when temperature was low and other factors were held constant. My results indicate that while ADM and distance of grass carp from the nearest shoreline may not vary seasonally, the depth of water occupied by grass carp does.

Hydrodynamic processes were related to all aspects of fish behavior measured in Lake Gaston. These results suggest that grass carp behavior is closely tied to flow dynamics in reservoirs used for hydropower. Lake elevation was an important factor for predicting both the distance of grass carp to the nearest shoreline, and ADM of grass carp. Outflow was important in predicting the water depth in which grass carp were located. Fish generally moved more and were located closer to shore when lake elevation was high. This behavior suggests that as the

total surface area of the lake is increased through water retention, grass carp move with rising water. These results make intuitive sense because a greater surface area of water results in increased availability of near-shore habitat where food resources are most abundant. The fact that lake elevation was not an important predictor in most of the best models of depth indicates that fish must have been moving inward toward shore in order to maintain their position in the water column during periods of increased lake elevation. This behavior may be beneficial for weed control in the lake because it allows grass carp to access areas that would otherwise be too shallow for them to enter (but not too shallow for hydrilla to grow in) during periods of lower water level.

The primary purpose of Lake Gaston is production of hydropower, and as such water release from the reservoir is governed by primarily by energy demand. However, Kerr Reservoir, the primary input of water for Lake Gaston, is a flood control reservoir. Thus, water release from the Kerr Dam into Lake Gaston is regulated primarily by rainfall and secondarily by the need to maintain water levels in Lake Gaston. As a result of the different purposes of the Kerr and Gaston Dams, flow dynamics differ in the upstream and downstream ends of Lake Gaston. The differences in flow dynamics between the upstream and downstream ends of Lake Gaston may affect fish behavior differentially at opposite ends of the reservoir. When outflow from the Gaston Dam was high and all other factors were held constant, fish moved less and were found in deeper water, suggesting that fish moved away from areas that hydrilla could occupy. Conversely, when lake elevation was high, grass carp appeared to be restricted in movement and distribution (depths and shoreline orientation) to areas suitable for hydrilla growth. These contrary results may be due to differences in flow regimes between ends of the reservoir, as regime is determined by inflow from the Kerr Dam in the upper reservoir and

release from the Gaston Dam in the lower reservoir. As an example, grass carp were found further from shore in the downstream end of Lake Gaston throughout this study and higher outflow also corresponded to greater depths occupied by grass carp. Based on the results of my study, it seems that outflow may be more important in determining fish behavior in the lower reservoir than hydrodynamic processes upstream. This speculation is further supported by the fact that the only difference in the two best models of ADM was the inclusion of either inflow or outflow. According to model-fit statistics, the two models provided virtually the same fit to the data.

As this study relies heavily on correlation, I have no way of prescribing cause and effect to the relationships between flow dynamics (or other predictors) and grass carp behavior. However, as an exploratory study, I have been able to identify specific interactions between grass carp behavior and their environment that warrant further investigation. One of the aspects of grass carp behavior illustrated in this study that warrants further investigation is behavioral relations to flow dynamics. The limited flow dynamics of hydropower reservoirs may make them more suitable for grass carp use than the more-variable flow dynamics of flood control reservoirs. In general, the elevation of Lake Gaston varies little over any period, fluctuating only ± 15 cm in a given day (Pearsall et al. 2005). The constant demand for energy and drinking water from Lake Gaston generally balance input from Kerr Dam, and flow in Gaston is regulated to pass water from Kerr reservoir with minimal elevation change (Pearsall et al. 2005). While Gaston varies little in lake elevation, Kerr Reservoir may vary by as much as 3-6 m in a given day (Pearsall et al. 2005). More-variable flow regimes in flood-control reservoirs could result in more-extreme changes in grass carp behavior. Research regarding these changes is lacking in the literature, and should be a focus of future grass carp telemetry research. Knowledge of these

relationships could be useful in risk assessments concerning the use of grass carp in hydrilla-control plans (e.g. Zajicek 2008).

I was able to identify relationships between grass carp behavior and several environmental factors in Lake Gaston using radio telemetry that provide areas of focus for future researchers. Because of the number of fish studied, and the span of this study, these relationships should be useful in understanding how fish behavior might affect management of grass carp in Lake Gaston. Grass carp were found in areas of the lake suitable for hydrilla growth the vast majority of the time I followed them. Within these areas, grass carp occupied near-shore areas with water depths suitable for hydrilla growth. As grass carp moved out of stocking areas in their second year, they continued to use habitats in which hydrilla could grow. These behaviors suggest that grass carp should be a useful tool for hydrilla control at Lake Gaston. There may be differences in grass carp behavior between the upstream and downstream ends of Lake Gaston that could be used to improve management decisions, such as locations and timing for grass carp stocking. In general, grass carp stocked in the upper reservoir appeared to occupy areas suitable for hydrilla growth more often in this study. Furthermore, grass carp behavior appeared to be affected more by hydrodynamic processes in the downstream end of the reservoir. Due to the differences observed in fish behavior between different ends of the reservoir, I recommend that future research in Lake Gaston evaluate changes in other aspects of grass carp ecology between the upper and lower reservoir.

Chapter 3: Variation in age-1 survival of triploid grass carp in a large reservoir

Abstract: Grass carp *Ctenopharyngodon idella* have been introduced throughout the world due to their utility as a biological control of noxious weeds. Where intermediate control is the objective of weed-management plans, successful management is dependent upon knowledge of grass carp population dynamics. While methods of estimating grass carp survival have been developed, they do not account for variation in survival between ages of grass carp. Better knowledge of age-specific survival at young ages may improve stocking models of grass carp survival. Furthermore, by understanding factors that affect survival at early ages, the cost of weed management might be decreased, and the effectiveness of stocking grass carp increased. I used known-fate models to estimate age-1 survival of radio-tagged grass carp in a large reservoir, Lake Gaston, based on encounter histories from telemetry data. Survival of age-1 grass carp in the reservoir varied over time and by stocking location. According to the best model developed in this study, survival of age-1 grass carp in Lake Gaston varied throughout the year, and the probability of an individual grass carp surviving to the end of its first year (\pm SE) was $0.57(\pm 0.10)$. According to the second-best model developed in this study, grass carp survival varied between stocking locations, and was twice as high in the upper reservoir (0.87 ± 0.09) than in the lower reservoir (0.43 ± 0.11). The differences in survival between stocking locations suggest that the cost-effectiveness of grass carp stocking could be improved by focusing stocking efforts in specific regions of Lake Gaston. Furthermore, none of the models developed in this study that incorporated the effects of size (length and weight) or condition factor accounted for a meaningful amount of the total model weights. These results suggest that costs of grass carp stocking could be reduced in Lake Gaston by using a smaller minimum size (352 mm, TL) than is commonly referred to in the literature (450 mm, TL). My

results also suggest that factors that could potentially influence grass carp survival should be considered before stocking. As fish stocking occurs, the type of information gathered and presented in this study can be used to better focus weed management efforts.

Introduction

Sterile, triploid grass carp *Ctenopharyngodon idella* have proven an effective biological control of invasive weeds such as hydrilla *Hydrilla verticillata* in many systems (Chilton and Muoneke 1992; Bonar et al. 1993a; Schramm and Brice 1998; Kirk and Henderson 2006; Pipalova 2006; Chilton and Magnelia 2008). Successful management of grass carp is based on thorough understanding of population parameters such as fish growth and survival (Clapp et al. 1993; Morrow et al. 1997; Kirk et al. 2000; Kirk and Socha 2003), particularly when the goal of weed control is some target level of infestation intermediate between complete eradication and no control (Chilton and Magnelia 2008). In the case of triploid grass carp, survival rates alone determine the rate of change in population size since natural reproduction is unlikely (Chilton and Muoneke 1992; Pipalova 2006) and immigration or emigration are also unlikely (Hightower et al. 2001). When survival is known, in combination with growth, managers can estimate the number and biomass of fish in a system (e.g., Morrow et al 1997) as well as the number of years that grass carp might persist after stocking (Kirk et al. 2000).

Reliable, non-lethal methods for aging grass carp have not been developed, so the only fish from which age-specific survival can be directly estimated are those fish marked at or prior to stocking. Indirect methods of mortality estimation, such as catch-curve analysis (Chapman and Robson 1960), have been used to estimate average annual survival of grass carp from catch data (Morrow et al. 1997; Kirk et al. 2000). However, grass carp collection does not always meet assumptions of catch-curve analysis such as equal vulnerability to gears between age classes. Where the assumptions of catch-curve analysis are not met, average annual survival can be estimated from other indirect methods if von Bertalanffy growth parameters are known (Pauly

1980; Jensen 1996). While the above techniques provide reasonable estimates of average, annual survival, none accounts for variation in survival between ages.

Due to difficulties capturing grass carp (Colle et al. 1978; Schramm and Jirka 1986; Chilton and Muoneke 1992; Bonar et al. 1993b), classical mark-recapture methods for estimating grass carp survival often result in biased or incorrect estimates of population size, even in small systems (Colle et al. 1978; Stott and Russell 1979). Recent advances in biotelemetry and computing technology have resulted in reliable means for estimating survival from capture-mark-recapture studies of radio-tagged animals (Pollock et al. 1989; Pollock et al. 1995; Pine et al. 2003). While these methods have been widely applied to wildlife populations (Pine et al. 2003), they have only recently been applied in fisheries management (Hightower et al. 2001; Heupel and Simpendorfer 2002; Pollock et al. 2004; Waters et al. 2005; Thompson et al. 2007). These methods have not been applied to estimate survival of grass carp.

Using radio-telemetry methods to estimate survival of age-1 grass carp stocked in a large reservoir could provide information useful for guiding management decisions. The primary objective of this study was to estimate the annual survival of age-1 grass carp stocked in a large, southeastern reservoir. As a secondary objective, I characterized relationships between age-1 survival and factors that may affect survival. The results of this study will be useful for validating or refining age-1 survival of grass carp estimated with other methods. Information from this study will be useful in identifying key factors affecting the cost and effectiveness of grass carp stocking plans.

Methods

Study site

Lake Gaston, located on the border of North Carolina and Virginia, is a large (8,500 ha), impoundment on the Roanoke River (Figure 3.1). The lake was constructed by Virginia Power and Electric Company (Dominion Power in NC) for the primary purpose of generating hydroelectric power in 1963. It is bordered upstream by Kerr Reservoir, and downstream by Roanoke Rapids Lake. Lake Gaston supports a popular fishery that includes species such as largemouth bass, *Micropterus salmoides*, walleye, *Sander vitreus*, striped bass, *Morone saxatilis*, and several species of ictalurid catfishes. In addition, the lake provides opportunities for non-consumptive recreation and is a center of residential and economic development in the region (Richardson 2008). Finally, Lake Gaston is a major supply of drinking water for Virginia Beach residents (Cox 2007).

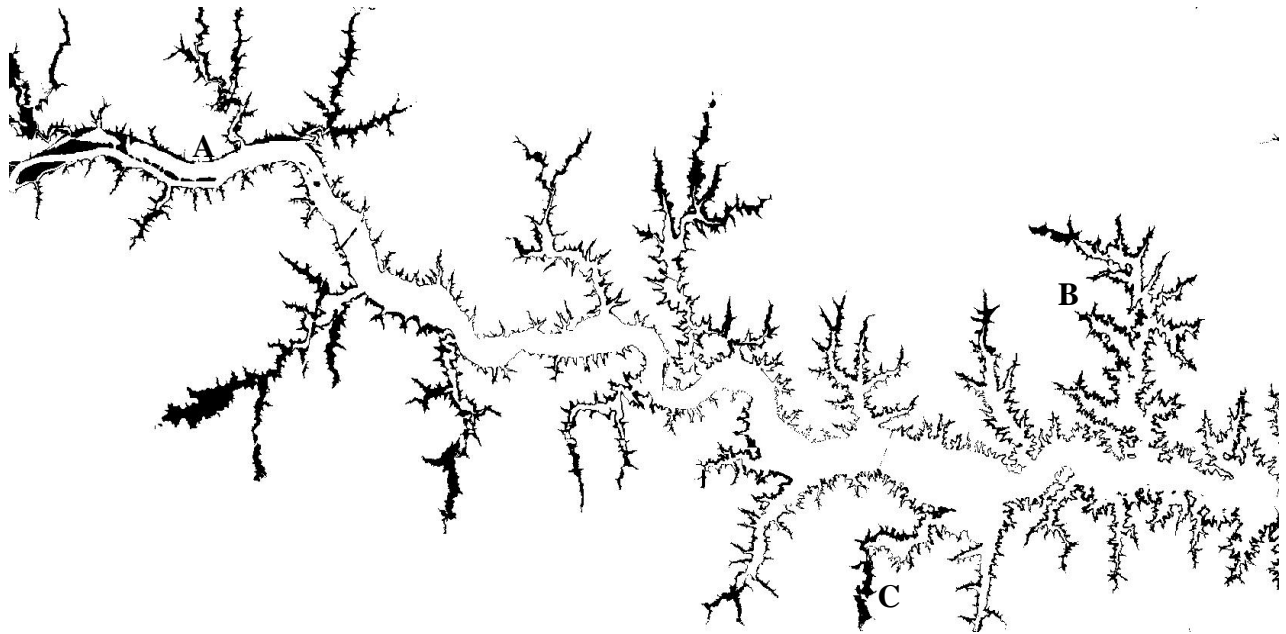


Figure 3.1.- Lake Gaston, North Carolina and Virginia showing grass carp stocking locations in the upper reservoir (A) and the lower reservoir (B and C).

Triploid grass carp were introduced into Lake Gaston in 1995 to control invasive hydrilla. Since then, about 75,000 triploids have been stocked incrementally to maintain a target density of <37 fish/ha (Table 3.1).

Table 3.1.- Stocking history of triploid grass carp in Lake Gaston.

Cohort	# Stocked
1995	20000
1997	680
1999	5000
2003	25392
2006	7000
2007	7720
2008	100
2009	6520
2010	7347

Current management of grass carp in the lake is precautionary, as complete eradication of submersed vegetation would be undesirable to some stakeholders (Richardson 2008). Grass carp are maintained at low levels, and are integrated with annual herbicide applications to control hydrilla. As grass carp biomass approaches target levels, small changes in estimates of fish survival could have drastic effects on the number of fish recommended for stocking. These effects could result in overshooting the target level of hydrilla in the lake, or in reverting to a situation where the appropriate level of control is not achieved. Because of the need to balance stakeholder values in Lake Gaston, precise information on the survival of grass carp at young ages is needed to guide future stocking decisions. Survival at age-1 may be affected by factors such as the size of fish at stocking or the stocking locations, which are under the control of the weed-management team at Gaston.

Radio tagging and telemetry

I used 40 fish radio tagged in April 2009 to estimate age-1 survival of grass carp. I tagged grass carp using two different procedures and depending on the size of fish being tagged, I used radio tags weighing 8 grams for 30 fish. Ten fish >1 kg each were fitted with 25-g tags. In no instance did the weight of radio tags exceed 2% of grass carp body weight, as recommended by Winter (1996). Fifteen grass carp were internally implanted with Model F1820 “grass carp” radio tags with trailing-whip antennae from Advanced Telemetry Systems (ATS Inc., Isanti, MN). In addition to a microprocessor-controlled, 14-d duty cycle and slow pulse rate of 30 ppm for extended battery life, the tags were equipped with mortality sensors. The mortality sensors were controlled with a mercury switch that activated after 12 hours of inactivity by quickening the pulse rate to 60 ppm. Fish were anesthetized with MS-222 in a holding tank prior to implant. Surgical tools were sterilized in a 10-ppt iodine solution. After they were anesthetized, fish were placed ventral side up in a v-shaped saddle. Water pumps were used to circulate anesthetic through the fish’s gills throughout the procedure. A small (2-cm) incision was made, offset slightly from the ventral line of the fish. Radio transmitters were tested for malfunctions before insertion. After testing, a transmitter was gently inserted through the incision. The incision was closed with three or four knots using non-absorbable, monofilament sutures. Fish were observed to recover before being released into the lake. Maximum time for implant surgery (including recovery) was about 15 minutes.

The remaining radio transmitters were modified for external attachment and attached to 25 fish. To modify radio transmitters for external attachment, four loops were secured to radio tags with epoxy in a rectangle about a single plane of the tag. Loops were formed by tying 8 knots around a sewing needle with 25-lb-test, monofilament line. Once the loops were secured

to the transmitter, epoxy was allowed to set for at least 24 hours prior to attaching the tags to grass carp. Fish were prepared for surgery as described above, except that they were placed ventral-side down in the v-shaped saddle. A rear-attachment wire (16-gauge sterilized surgical steel) was passed through the dorsal musculature, and then through two loops on either side of the radio tag. The radio tag was then secured by twisting the ends of the attachment wire 7 to 8 times above the tag. The same procedure was repeated about 5 cm anterior to the rear-attachment location. After the forward-attachment wire was tightened, the two wires were twisted together 8-10 times. The wires were cut and folded flat against the top of the radio tag, pointing backward.

Seven fish with internal transmitters and 13 fish with external transmitters were released in the lower reservoir. Eight fish with internal transmitters and 12 fish with external transmitters were released in the upper reservoir. Stocking locations for grass carp coincided with annual stocking locations used for non-radio-tagged fish (Figure 2.1).

After stocking, I attempted to locate all fish at least once per month for one year. Grass carp were radio tracked using boat-mounted Yagi antennae and a model R410 receiver from ATS. Monthly capture histories were constructed for each fish using binary coding. Since all radio-tagged grass carp survived the initial three months of this study, we used all fish to estimate survival. Binary capture histories were used in program MARK (White and Burnham 1999) to perform known-fate analyses using several candidate models. Known-fate survival models in program MARK are based on the Kaplan-Meier product limit estimator (Kaplan and Meier 1958- Equation 1) and are modified to estimate survival as a maximum likelihood estimate based on the product of individual likelihoods (Equation 2) where \hat{S}_t is survival to through t intervals (in equation 1), S_i is the maximum-likelihood estimate of survival in each interval, i , Θ

is the survival model for the t intervals (in Equation 2), n_i is the number of individuals alive and at risk of death at the start of the i^{th} interval and y_i is the number of surviving i^{th} interval

$$\hat{S}_t = \prod_{i=1}^t \left(\frac{y_i}{n_i} \right) \quad (1)$$

$$\mathcal{L}(\theta | n_i y_i) = \prod_{i=1}^t S_i^{y_i} (1 - S_i)^{(n_i - y_i)} \quad (2)$$

Animals that were not found in a given survey were censored (removed from likelihood estimation) for that time period, and if an animal died during the study, they were censored for the duration. A full description of this model and its assumptions is presented in Pollock et al. (1989). For my study, the primary assumptions of the known-fate models were:

- 1) Survival is equal between genders of fish;
- 2) Survival is independent for all fish;
- 3) Radio tags do not affect fish behavior or survival;
- 4) Censoring of individual fish is random; and
- 5) Fish movement patterns and mortality sensors can be used to determine if animals are alive or dead.

Model development and covariates

I developed multiple hypotheses a priori to determine which variables were most likely to influence age-1 survival of grass carp. The hypotheses fell into four general categories including spatial and temporal effects (variation in survival between months and stocking locations), effects of size (length, and weight), the effect of condition, and transmitter effects (tag weight and tagging method, and tag-weight-to-fish-weight ratio). I then developed known-fate survival models that corresponded to hypotheses to be tested. Survival models were structured

as generalized linear models using the logit link function in program MARK. Parameters in each model and their variances were estimated using maximum likelihood estimation. Likelihoods were based on the probability of observing individual encounter histories given the data. The likelihood of a fish surviving the duration of the study was determined as a product of individual likelihoods. The binomial variance for survival was calculated from the 2nd partial derivative of the likelihood with respect to survival using Equation 3, where n is sample size and \hat{S} is the maximum-likelihood estimate of survival. I performed model selection using information-theoretic methods based on Akaike's information criterion corrected for bias due to small sample sizes (AIC_c) and AIC_c weights (Burnham and Anderson 2002).

$$n\hat{S}(1 - \hat{S}) \quad (3)$$

Grass carp growth and survival have been shown to be influenced by the density of fish per area of aquatic weeds (Colle et al. 1978; Catarino 1997; Kirk et al. 2000). To incorporate this dependence in my models, I tested variation in survival between months, since hydrilla coverage in temperate systems varies throughout the year and is characterized by periods of growth, senescence, and re-growth. I hypothesized that survival would be time-dependent due to the seasonal nature of the hydrilla growth and other environmental variables that may affect grass carp survival. To test this hypothesis, I developed models that assumed survival either varied by month ($S_{time-dependent}$) or was constant throughout the year ($S_{constant}$). The time-dependent model used 10 intervals through 12 months. All intervals were 1 month long except the final interval, which was 2 months in length. Differences between the lengths of each interval were incorporated into program MARK.

Possible differences in survival between stocking locations may occur due to a host of factors. Some differences between stocking locations for grass carp in Lake Gaston that may

affect survival include mean channel width and depth, hydrilla growth, flow regimes, temperatures, and human impacts such as nutrient loading, spot treatment with herbicides, and recreational activities such as boating. The upstream end of the reservoir is generally more river-like than the downstream end. Throughout the upper reservoir, small creeks and backwaters make up a large portion of the physical habitat, while the lower reservoir mainly comprises large, open coves and main-channel habitat. In addition, the upstream end of the reservoir is less developed than the downstream end, and sees less recreational use than downstream sites. To test the effects of stocking location on survival I developed a known-fate model that allowed survival to vary between stocking locations ($S_{stocking\ location}$).

Previous research has shown a significant effect of grass carp length at stocking on fish survival (Shireman et al. 1978). The minimum size recommended for stocking in systems with Florida-strain largemouth bass is 450 mm (Shireman et al. 1978). The minimum length of grass carp radio tagged in our study was 352 mm. While Florida-strain largemouth bass are not present in Lake Gaston, there are a variety of potential predators that could consume grass carp larger than the minimum size recommended by Shireman et al. (1978). Potential predators of juvenile grass carp in Lake Gaston include striped bass, blue catfish, *Ictalurus furcatus*, and flathead catfish, *Pylodictis olivaris*. To determine if the size of grass carp stocked in Lake Gaston exposed fish to differential mortality, I included two measures of size in my models. As measures of size, I used total length (TL, mm) and weight (g) of radio-tagged grass carp. I developed models that allowed survival to vary by length (S_{length}) or by weight (S_{weight}).

I based the condition of fish on the Fulton condition factor (C) calculated from length and weight measurements (Anderson and Neumann 1996). The basis for including condition was that fish in better condition might have higher survival if a substantial amount of time passed

between stocking and annual hydrilla re-growth. To test this hypothesis, I developed a known-fate model that allowed survival to vary with fish condition ($S_{condition}$).

The general “rule of thumb” for tags used in fish telemetry studies is that tag weight should not exceed 2% of fish body weight (Winter 1996). In the past, fisheries professionals have recommended that such generalizations not be used to guide tagging decisions (Brown et al. 1999; Jepsen et al. 2002). Recent research has shown that the maximum ratio of tag weight to fish size should be based on study objectives, tagging methods, and life history of study organisms (Jepsen 2005). However, few studies actually evaluate the effects of tagging on fish behavior or survival (Jepsen 2005). In order to evaluate differences in fish survival due to tagging methods or tag weight, I developed known fate models that allowed survival to vary by tagging method ($S_{tag\ type}$) and by tag weight ($S_{tag\ weight}$). In order to incorporate the effects of tag burden on fish survival, I developed a known-fate model that allowed survival to vary by the ratio of tag weight to fish weight ($S_{tag:fish}$).

Results

The majority (87%) of the AIC_c model weights from this study were attributed to two models (Table 3.2). The two models showing the most support were the model that allowed survival to vary throughout the year ($S_{time-dependent}$), and the model that allowed survival to vary by stocking location ($S_{stocking\ location}$). A small amount of support was given to the models that incorporated weight and the tag-weight-to-fish-weight ratio, but support was less than 4% of the total AIC_c model weights for either model. None of the remaining of the models tested in this study showed a meaningful amount of support.

About 58% of the cumulative AIC_c model weight was attributed to the time-dependent model of survival, suggesting that grass carp survival varied significantly with time. Furthermore, support for the model that assumed constant survival was only 2% of the cumulative AIC_c weight. According to the time-dependent model, the probability of grass carp surviving the first year in Lake Gaston (\pm SE) was about 0.57 (\pm 0.10).

Table 3.2.- Results of known-fate model selection based on Akaike's information criterion corrected for bias from small sample sizes (AIC_c) for age-1 grass carp in Lake Gaston. Models are ranked based on AIC_c; and w_i is the model AIC_c weight.

Model	AIC _c	Δ AIC _c	w_i	K
<i>S</i> time-dependent	97.39	0.00	0.58	11
<i>S</i> stocking location	98.75	1.37	0.29	2
<i>S</i> tag:fish	102.76	5.37	0.04	2
<i>S</i> weight	103.26	5.87	0.03	2
<i>S</i> constant	104.21	6.82	0.02	1
<i>S</i> condition	104.76	7.38	0.01	2
<i>S</i> tag type	105.24	7.85	0.01	2
<i>S</i> tag weight	105.40	8.01	0.01	2
<i>S</i> length	105.69	8.31	0.01	2

Survival of grass carp in Lake Gaston appeared to vary between stocking locations (Figure 3.1). The second-best model of age-1 grass carp survival in Lake Gaston allowed survival to vary between stocking locations (*S* stocking location). This model comprised about 29% percent of the total AIC_c model weights. In the upper reservoir the probability of a grass carp surviving the first year was approximately 0.87 (\pm 0.09), while age-1 survival of grass carp stocked in the lower reservoir was about 0.43 (\pm 0.11).

Grass carp survival did not appear to be related to the tagging method or the weight of the tag used. None of the survival models that included effects of tagging accounted for more than

1% of the cumulative AIC_c model weights. All three models that incorporated tagging effects showed less support than the model that assumed no variability in survival ($S_{constant}$).

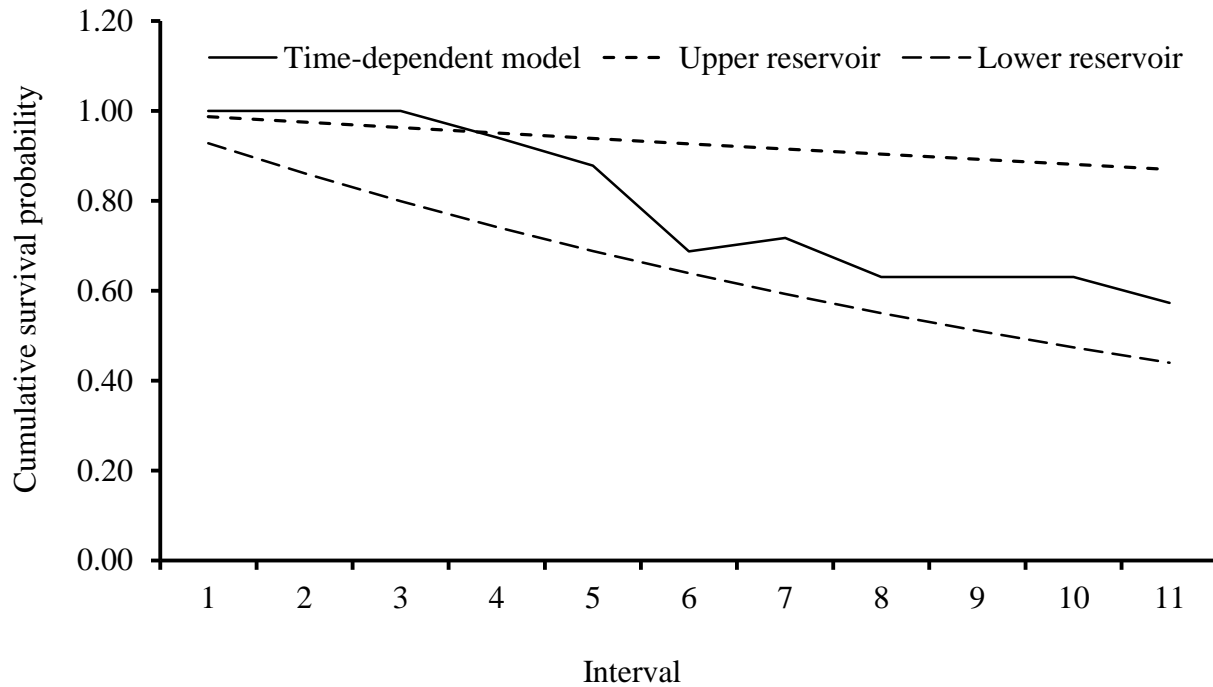


Figure 3.2.- Cumulative survival probabilities of grass carp in Lake Gaston according to the time-dependent model, and in separate ends of the reservoir as determined using the model that incorporated the effect of stocking location.

Discussion

I observed a substantial difference in grass carp survival between stocking locations in Lake Gaston. Survival of grass carp in the upper reservoir was more than double survival of fish stocked in the lower reservoir. One potential reason for the low survival of grass carp stocked in the lower reservoir is the amount of time fish spent in hauling trucks and holding tanks.

However, because all grass carp survived the first three months of the study, it seems unlikely that survival was affected by hauling stress. A more-reasonable explanation is that environmental differences exist between the upper and lower reservoir that contribute to better

survival of grass carp in the upper end. The most-obvious factor that might affect survival between stocking locations is food availability. Direct estimates of hydrilla coverage in Lake Gaston do not separate the reservoir into upper and lower ends. Though, in general, the largest and most-dense stands of hydrilla are found in the shallows of the upper reservoir (Remetrix 2009, 2010, 2011). Due to strong environmental gradients in reservoirs, upstream and downstream areas differ substantially with regard to physical and chemical habitat and distributions of established fish populations tend to be predictable (Gido et al. 2002). In Lake Gaston, like many large reservoirs, habitat in the upper reservoir is more riverine than in the lower reservoir, and is characterized by numerous small creeks and expansive, shallow, back-water areas. The lower end of Lake Gaston is more lentic than the upper reservoir, and is predominantly made up of large, open coves and main-channel habitat. Because grass carp are native to large river systems (Chilton and Muoneke 1992), it is conceivable that differences in habitat between stocking areas could impact grass carp survival. This is especially true if age-1 survival of grass carp is tied to availability of specific habitats such as small creeks and shallow flats.

Shoreline development and human population density generally are much higher in the lower end of the reservoir. One major difference in anthropogenic influence between stocking areas is that the lower reservoir sees higher levels of boat and jet-ski traffic than the upper reservoir. Studies of grass carp movement and habitat use in Lake Gaston have shown that grass carp were located further from shore in the lower reservoir than in the upper reservoir (chapter 1). It is possible that factors such as boat traffic and shoreline development may influence grass carp behavior and survival in Lake Gaston. Based on my results, it seems likely that the

differences in habitat and human use can also lead to differences in grass carp survival between stocking locations.

Survival of age-1 grass carp in Lake Gaston was not related to the size of fish stocked. My results imply that grass carp either are currently stocked at sizes sufficient to minimize predation, or that grass carp of all sizes stocked in Lake Gaston are equally vulnerable to predation. Since some grass carp used in this study were >500 mm and weighed nearly 2 kg, I suspect that if there is no difference in survival due to size, it is because predation risk is minimized by sufficiently large stocking sizes in Lake Gaston. A minimum stocking size of 450 mm for grass carp was recommended to eliminate predation in lakes with Florida-strain largemouth bass (Shireman et al. 1978). The minimum size of grass carp used in my study was 352 mm. Since stocking size had no detectable effect on grass carp survival in Lake Gaston, I speculate that a stocking size of 352 mm is sufficient to minimize losses to predation in this system. Stocking smaller grass carp is more economical than stocking large fish due to decreased costs of growing fish to smaller sizes (Chilton and Muoneke 1992). By using a smaller minimum size for grass carp at stocking, the cost of stocking grass carp in Lake can be reduced.

Neither the weight of tags, tag burden, nor the type of surgery had significant effects on grass carp survival. These results indicate that the assumptions of known-fate models regarding the effects of radio tags on the survival of individuals were satisfied. Furthermore, the results of the tagging study serve as a form of verification that neither tagging methods nor tag weights affected the interpretation of other results (Jepsen 2005). In general, I conclude that tags weighing less than 2% of grass carp body weight do not appear to affect fish survival. Because the effects of tags on fish behavior and survival cannot be determined a priori in any telemetry

study, I suggest that the 2% rule (Winter 1996) is a reasonable starting point for telemetry studies of grass carp 352-573 mm TL. However, I support the recommendations of Jepsen (2005) that in the future, effects of tagging should be taken into account during analysis.

In Lake Gaston (and many other management scenarios), stocking locations are often decided based on political rather than biologically meaningful considerations. Based on the results of this study, the cost of stocking grass carp in Lake Gaston could be substantially reduced. In general, the stocking size of grass carp needed to reduce losses to predation in Lake Gaston (352 mm, TL) is smaller than the size of 450 mm recommended in the literature (Shireman et al. 1978) so the cost of stocking in Lake Gaston could be reduced by using smaller fish at stocking. In the future, differences in habitat should be taken into account when stocking locations are decided. Grass carp stocked in the upper reservoir have significantly higher survival rates than grass carp stocked in the lower reservoir. Grass carp appear to associate with target areas more closely than fish stocked in the lower reservoir (chapter 1). Based on the results of behavioral studies of grass carp in Lake Gaston, it appears that during the second year in Lake Gaston, stocked grass carp move to and from target areas throughout the lake and may move the entire distance of the lake (chapter 1) thus reducing the need to spread stocking locations throughout the lake. These results suggest that managers may be able to further reduce the cost of weed control by stocking grass carp only in the upper reservoir. Conversely, the cost of continuing to stock in the lower reservoir could increase due to decreased survival and the need for more fish at stocking to maintain target densities.

Chapter 4: Growth and population dynamics of grass carp incrementally stocked for biological control of hydrilla

Abstract: In many aquatic weed-control plans that use grass carp, the goal of weed control is some level intermediate between eradication and no control. To effectively manage biological controls such as grass carp for intermediate weed control, managers must have an understanding of population dynamics and processes over the long term. The purpose of this study was to characterize growth, mortality, and associated population parameters of long-lived, triploid grass carp that were incrementally stocked for biological control of hydrilla in a large reservoir. Grass carp were collected 2006-2010 from Lake Gaston (VA/NC) by specially permitted bowfishers. Grass carp collected from Lake Gaston ranged in age 1-16 years. Growth of grass carp in Gaston was described by the von Bertalanffy growth function as $L_t = 1297(1 - e^{-0.1352(t+1.52)})$. I estimated mortality from the von Bertalanffy growth parameters using methods based on growth, temperature, and age; and with each mortality estimate I estimated population size and standing biomass of grass carp. Estimates of instantaneous mortality ranged from 0.20 to 0.25 depending on the method used. Use of age-specific mortality rates produced lower estimates of grass carp numbers and standing biomass in Lake Gaston than did the use of a single, instantaneous mortality rate for all ages. I determined that growth of grass carp slowed considerably after the fourth year and that slowed growth, in combination with changes in mortality, resulted in a decrease in the amount of hydrilla controlled by a given cohort after four years in Lake Gaston. This phenomenon resulted in an approximately linear relationship between the biomass of grass carp at year i and hectares of hydrilla at year $i+3$. Based on this relationship, I predicted that the biomass of grass carp necessary to reduce hydrilla coverage to the target level of 120 ha in Lake

Gaston is about 91,184 kg ($\pm 38,146$ kg) and that the current biomass of grass carp in Lake Gaston is about 108,073 kg ($\pm 3,609$ kg). I conclude that grass carp biomass is at or near levels that should reduce hydrilla coverage to 120 ha between 2013 and 2018. I recommend that future grass carp stocking rates used to maintain target fish density in Lake Gaston be based on standing biomass estimated from age structure and growth of grass carp, instead of numbers of fish.

Introduction

Grass carp *Ctenopharyngodon idella* have been widely stocked for biological control of aquatic vegetation in the United States since introduction in 1963 (Mitchell and Kelly 2006). The species has been proven an effective control agent for invasive aquatic weeds such as hydrilla *Hydrilla verticillata* which is a highly preferred food source for grass carp (Allen and Wattendorf 1987; Chilton and Muoneke 1992; Kirk et al. 2000). Classical approaches to biological control of hydrilla with grass carp often involve a single, large, stocking event. In many situations, grass carp either provide inadequate control of vegetation (Baker et al. 1974; Kirk 1992; Killgore et al. 1998), or completely eradicate vegetation from systems (Stott and Robson 1970; Bettoli et al. 1993; Killgore et al. 1998; Schramm and Brice 1998). Variability in potential outcome has resulted in stocking rates for grass carp that range from 2 to 500 fish per vegetated hectare (Kilgen and Smitherman 1971; Allen and Wattendorf 1987; Kirk et al. 2000; Bonar et al. 1993, 2002). In most cases, weed-management goals target some level of intermediate control of noxious weeds (Bonar et al. 2002). To this end, a more-effective means of intermediate hydrilla control by grass carp might be achieved through incremental stocking in combination with low-level herbicide application (Chilton and Magnelia 2008). This approach allows fisheries managers to make intermediate adjustments to stocking rates so that fish density can be maintained at a desired level (Chilton and Magnelia 2008). Knowledge of growth, mortality, and longevity of grass carp is an essential component of any long-term, hydrilla-control plan that utilizes the species (Kirk et al. 2000; Kirk and Socha 2003).

Research has shown that mortality and growth rates of grass carp vary by geography, climate, availability of food, and age (Chilton and Muoneke 1992). State and federal agencies have developed software programs that predict the potential impacts of grass carp for up to 10

years based on a host of factors (e.g., Stewart and Boyd 1999). Previous studies documented methods for collecting and aging grass carp in the Santee-Cooper system, and estimated mortality of grass carp using catch-curve analysis (Morrow et al. 1997; Kirk et al. 2000). The Santee-Cooper population of grass carp had an estimated life expectancy of approximately 11 years and eradicated all submersed vegetation in the first five years of stocking (Kirk and Socha 2003). However, studies have shown that grass carp may live up to 21 years in native rivers where food is plentiful (Gorbach 1961), and one individual was found in the United States that was 33 years old (Cudmore and Mandrak 2004). While some life-history studies have been conducted on sterile, triploid grass carp (e.g., Morrow et al. 1997; Kirk et al. 2000), little information exists regarding population characteristics from established, long-lived populations that have not eradicated all vegetation.

Hydrilla was first identified in Lake Gaston, North Carolina and Virginia, in 1992 (Ryan et al. 1995). Initial coverage was about 10 ha, and coverage peaked at 1,364 ha in 2003 (Williams et al. 2008). Incremental grass carp stocking has been integrated with annual fluridone applications to control hydrilla in Lake Gaston since 1995 (Rob Richardson, North Carolina State University, Raleigh, NC, personal communication). By 2010 hydrilla coverage was reduced to approximately 428 ha (Remetrix 2011). The management goal for hydrilla control in Lake Gaston is, “to develop and maintain a healthy lake ecosystem based on a diverse plant community dominated by native species” (Mike Smart, US Army Corps of Engineers Research Division, personal communication). In order to achieve this goal, one objective of management is to reduce hydrilla coverage to 120 ha by 2012. This 120 ha is designed to serve as a buffer for expected grass carp grazing, and allow native aquatic vegetation to re-establish (Mike Smart, US Army Corps of Engineers Research Division, personal communication). The

target density for grass carp standing stock currently is 37 fish/vegetated ha (Rob Richardson, North Carolina State University, personal communication).

The objectives of this study were to characterize the growth and mortality of a long-lived grass carp population from fish collected from Lake Gaston and to estimate the current standing stock of grass carp in Lake Gaston. In order to assess the usefulness of standing-stock estimates, a further objective was to compare predicted population characteristics resulting from several different mortality estimates. I used the standing-stock estimates to characterize the relationship between grass carp density and hydrilla coverage in Lake Gaston.

Methods

Fish collection and aging

Specially permitted, volunteer bowfishers collected 243 grass carp from Lake Gaston 2006-2010. I measured total length (TL) of individual grass carp to the nearest millimeter, and weight to the nearest gram. Whole fish were stored in deep freezers, and allowed to thaw for 1-2 days before otolith removal. I exposed lapilli otoliths by removing a section of the supraoccipital bone (Morrow et al. 19Gra7). Otoliths were removed with tweezers, cleaned, and stored dry in coin envelopes. Otoliths were mounted to microscope slides with Crystal Bond 509 mounting adhesive (T-E-Klebetchnik, Hannover, Germany) such that the anterior end of the otolith protruded perpendicular to the long plane of the slide when the slide lay flat. I sanded otoliths using high-grit sandpaper on a grinding wheel or by hand, holding the slide and sanding from the anterior end toward the posterior end of the lapillus. As annuli became apparent under a stereomicroscope, I took pictures of the otoliths at short intervals to minimize the likelihood that annuli were not observed due to otolith preparation. I used an Olympus Q Color3 digital camera

(Model no. 01-QCOLOR3-RTV-CLR-10) mounted atop an Olympus stereomicroscope (model no. SZ61) to photograph otoliths (Olympus America, Inc., Center Valley, PA). From the images, I estimated ages of individual grass carp based on annular ring formation.

Two to three individuals from the Virginia Department of Game and Inland Fisheries (VDGIF) read otoliths of grass carp collected 2006-2008, and came to a consensus on the estimated age of individual fish. I read all otoliths independently twice, except those collected in 2008, with at least one month between aging events. Otoliths collected in 2008 were not aged by me. Otoliths collected 2009-2010 were not aged by VDGIF personnel.

I tested the effects of personnel (reader) and aging event on the age assigned to each fish using a general linear model (Zar 1999). Individual fish were included in the model as random effects. I used variance components to determine the proportion of variance in assigned ages due to different personnel and aging events. I tested for differences in the ages assigned to each fish between reader and event using two-sample t-tests (Zar 1999). The general linear model used to describe variation in the age assigned to each fish suggested that less than 1% of the variation in the age assigned to each fish was due to reader or aging event. No differences were found in the age assigned to fish between readers or aging event. Therefore, final ages of individual grass carp were assigned by using the first age estimated for each fish so that age assignment was systematic.

Growth of grass carp

After ages were assigned, I measured the radius (mm) of each otolith using Image Pro Plus software (Media Cybernetics, Inc., Bethesda, MD). I made measurements from the core to each increment and to the margin for back calculation using imaging software. I used the

Fraser-Lee method to back-calculate lengths at each age (Devries and Frie 1996). I characterized the relationship between otolith radius (S_c) and fish length at capture (L_c) using simple linear regression. The intercept parameter of the regression equation was used as an estimate of the correction factor (a) in Equation 1, and was estimated using the entire size-range of grass carp collected from the lake (Devries and Frie 1996).

$$L_i = \frac{L_c - a}{S_c} S_i - a \quad (1)$$

I back-calculated length at each age (L_i) for nearly all of the grass carp collected from Lake Gaston. Some otoliths were not used for back calculation because they were malformed, or annuli grew irregularly. In such instances, I used the other paired lapillus or excluded the fish from back-calculation analyses. I used analysis of variance (ANOVA) to determine the effect of age on growth rate (Zar 1999). I tested for differences in growth between ages using Tukey-Kramer pair-wise comparisons of means (Zar 1999) to determine at what age grass carp growth became asymptotic.

I estimated von Bertalanffy growth parameters (von Bertalanffy 1938) iteratively from raw, age-length data and plotted a von Bertalanffy growth curve using R software (R Development Core Team 2008). I used preliminary values of parameter estimates obtained using mean length at age in program FAST as starting values for the final fit (Slipke and Maceina 2001). Parameter estimates for the growth curve were reported in the form of Equation 2, such that

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \quad (2)$$

where L_t is the mean length of fish at age t , L_∞ is the theoretical maximum length of fish in the population, K is a growth parameter, and t_0 is the arbitrary origin of the equation (von Bertalanffy 1938). I estimated 95% confidence intervals (CI) for the parameter estimates using

bootstrap methods iterated 20,000 times. I predicted mean length at age, and constructed 95% CI using the bootstrapped results in program R.

I estimated the relationship between length and weight by the power function $W=aTL^b$ for all grass carp collected from Lake Gaston (Ricker 1975). I used the equation to predict the weight of grass carp at each age from back-calculated lengths at age (Anderson and Neumann 1996). I used the predicted weight at each age, in combination with mortality, to estimate biomass of grass carp in Lake Gaston.

Mortality and associated population parameters

Based on my preliminary analyses, grass carp collection in Lake Gaston did not meet assumptions of equal catchability among age classes or between years required for catch-curve analysis, so I used three simple alternatives to estimate mortality of grass carp based on von Bertalanffy parameters. I used multiple methods to comparatively characterize the precision of multiple approaches to estimating mortality. I used a hierarchical approach to estimate 95% confidence intervals (CI) for mortality estimates using each method from bootstrapped results of von Bertalanffy growth parameter estimation. Since changes in the size of triploid grass carp populations depend entirely on mortality, I predicted population size and biomass of grass carp based on each of the three mortality estimates. I present the models below in order of increasing complexity.

Growth-dependent mortality.- Jensen (1996) demonstrated that the relationship between natural mortality (M) and the von Bertalanffy growth coefficient (K) could be expressed by

Equation 3. According to this method, mortality is predicted based solely on the growth rate of fish.

$$\hat{M} = 1.50K \quad (3)$$

I used Equation 3 to estimate average, annual mortality (\hat{M}) across all ages. I used the value of \hat{M} predicted by Equation 3 to estimate the number of grass carp at each age remaining in Lake Gaston at the start of each year ($N_{t,i}$) using Equation 4, where R_i is the number of fish stocked in time i . I estimated population size at the start of each year (\hat{N}_i) according to Equation 5.

Equation 6 was used to estimate annual biomass of grass carp in each age class ($B_{t,i}$) at the start of each year. I estimated standing biomass (\hat{B}_i) of grass carp in Lake Gaston at the start of each year using Equation 7.

$$N_{t,i} = N_{t-1,i-1}e^{(-\hat{M})} + R_{t,i} \quad (4)$$

$$\hat{N}_i = \sum N_{t,i} \quad (5)$$

$$B_{t,i} = N_{t,i}W_t \quad (6)$$

$$\hat{B}_i = \sum B_{t,i} \quad (7)$$

Temperature-dependent mortality.- Pauly (1980) estimated fish mortality based on interrelationships between maximum size (L_∞), growth rate (K), temperature (T) and natural mortality using 175 fish stocks. Temperature used for mortality estimates from this method can be based on average annual water temperature or on air temperature. I used average annual water temperature at Lake Gaston as measured in telemetry studies of grass carp. I estimated average mortality of grass carp of all ages (\hat{M}) in Lake Gaston from Equation 8. I used the same methods to estimate annual population size and biomass from temperature-dependent mortality as I did for growth-dependent mortality.

$$\log \widehat{M} = .654 \log K - .28 \log L_{\infty} + .463 \log T \quad (8)$$

Age-dependent mortality. - I used methods developed by Chen and Watanabe (1989) to estimate age-specific natural mortality rates of grass carp in Lake Gaston (M_t) based on maximum-observed age (t_{max}), K , and t_0 where a_0 , a_1 , and a_2 are constants pertaining to senescence described mathematically by Chen and Watanabe (1989) (Equation 9). I used Equation 10 to estimate the number of grass carp in Lake Gaston at each age from 1995 to 2010 ($N_{t,i}$), and Equation 5 to estimate the annual population size for grass carp of all ages. Biomass was estimated using Equations 6 and 7. I estimated \widehat{M} in the age-dependent model as mean M_t across all ages and used the resultant value of \widehat{M} to comparatively assess the precision of mortality estimates from the three models described above.

$$M_{(t)} = \begin{cases} \frac{K}{1 - e^{-k(t-t_0)}}, & t < t_{max} \\ \frac{K}{a_0 + a_1(t-t_{max}) + a_2(t-t_{max})^2}, & t \geq t_{max} \end{cases} \quad (9)$$

$$N_{t,i} = N_{t-1,i-1} e^{(-M_t)} + R_{t,i} \quad (10)$$

I used paired-t tests to determine differences between model-estimates of annual population size (\widehat{N}_i) (Zar 1999). I tested the relationship between grass carp numbers and biomass predicted from each model and hydrilla coverage using simple linear regression (Montgomery et al. 2006). Hydrilla coverage estimates used in this study were contracted by the Lake Gaston Weed Control Council on an annual basis 199-2011. Because there was a time-lag expected between grass carp stocking and subsequent effect on hydrilla coverage, I tested the

relationship between model-estimated numbers and standing biomass of grass carp in year i and hydrilla coverage in years i , $i+1$, $i+2$, and $i+3$. A maximum time-lag scenario of three years was used because preliminary analyses suggested both growth and mortality of grass carp stabilized after age four. I used Mallow's C_p , PRESS, and r^2 -adjusted to rank the fit of the regression equations resulting from each model (Montgomery et al. 2006). I used the best model, as determined by model-fit statistics, to predict the biomass of grass carp needed to reduce hydrilla coverage in Lake Gaston to 120 ha.

Results

Fish collection

Grass carp collected by bowfishers represented ages 1-16 in Lake Gaston (Table 4.1). All stocking cohorts 1995-2010 were represented in the sample. Total length (TL) of individual grass carp collected ranged from 417 to 1350 mm. Grass carp collected in this study weighed 0.95-34.0 kg.

Table 4.1.- Stocking years, number of fish stocked, and annual catch of grass carp by bowfishers in Lake Gaston 2006-2010.

Cohort	# Stocked	Number caught per year					Total
		2006	2007	2008	2009	2010	
1995	20,000	12	25	9	17	22	85
1997	680	2	1	5	2	5	15
1999	5,000	0	2	1	3	12	18
2003	25,392	22	14	4	6	7	53
2006	7,000	1	7	7	16	9	40
2007	7,720	0	0	0	7	14	21
2008	100	0	0	0	0	9	9
2009	6,520	0	0	0	0	2	2
2010	7,347	0	0	0	0	0	0
Total	79,759	37	49	26	51	80	243

Growth of grass carp

Grass carp growth rate (mm/yr) in Lake Gaston (Figure 4.1) decreased significantly with age ($df=15$, $F=516.8$, $p<0.001$). Parameters estimates for the von Bertalanffy growth function describing grass carp growth in Lake Gaston are listed in Table 4.2. After age 4, the difference in growth rate between one age and the next was not significantly different. The relationship between length (TL) and weight (W) of grass carp was described as $W=.0000325387TL^{2.8746917}$ ($r^2=0.91$, $df=242$ $F=1794$, $p=0.0001$), suggesting that grass carp became less rotund as length increased (Anderson and Neumann 1996). The relationship between weight (W) and age (t) was linear and was described as $W=1448+1623t$ ($r^2=.99$, $df=15$ $F= 1358.1$, $p<0.001$).

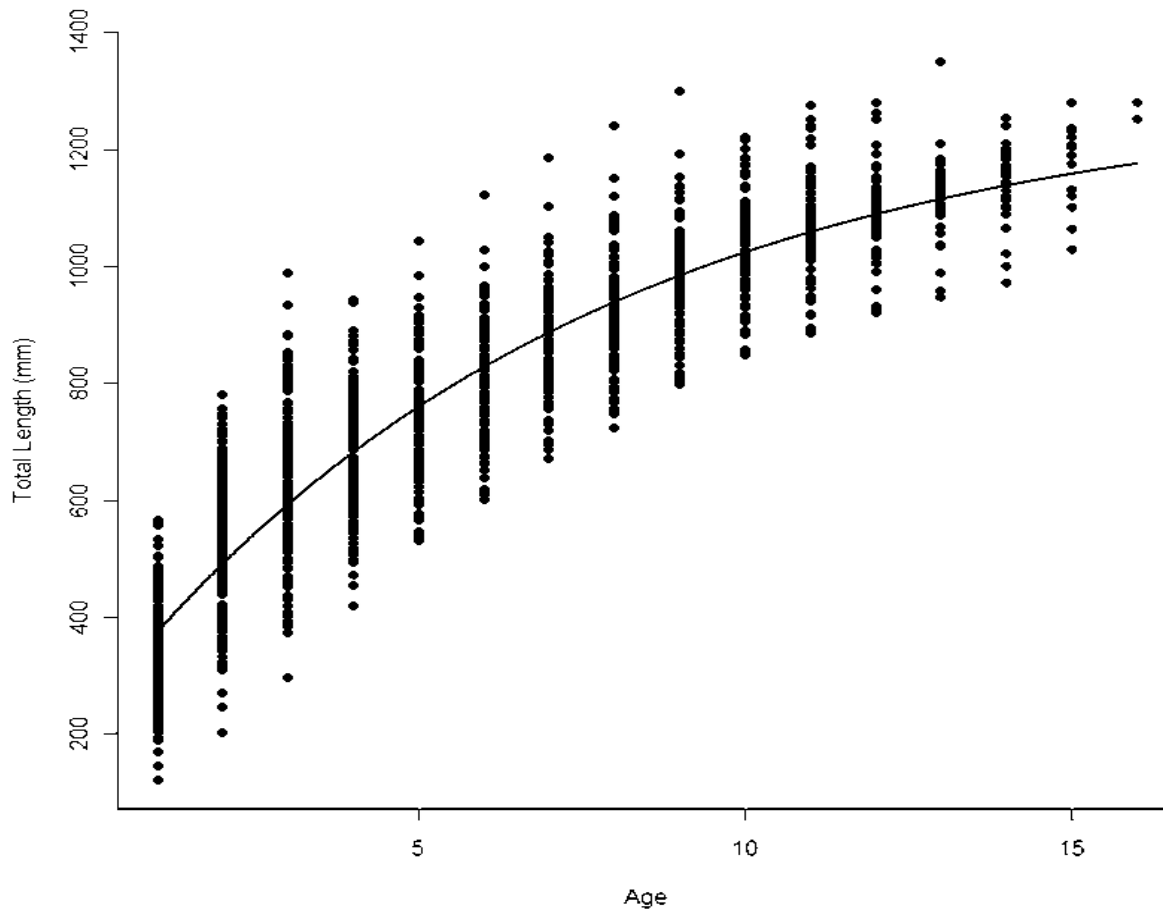


Figure 4.1.- Plot of the von Bertalanffy growth curve estimated for grass carp collected from Lake Gaston by bowfishers. The equation for the curve is $L_t = 1297(1 - e^{-0.1352(t+1.52)})$, where L_t is length at age t . The convergence criteria for von Bertalanffy parameter estimation were met with four iterations ($p < 0.0001$).

Table 4.2.- Estimates, standard error (SE), 95% confidence limits (CL), and test statistics for parameterization of the von Bertalanffy growth function describing growth of grass carp collected from Lake Gaston.

Parameter	Estimate	SE	Lower 95% CL	Upper 95%CL	t	p>t
L_{∞}	1297	24.160	1253	1348	53.66	<0.0001
K	0.135	0.007	0.122	0.149	19.67	<0.0001
t_0	-1.52	0.112	-1.75	-1.31	13.54	<0.0001

Mortality and associated population parameters

The estimate of \hat{M} derived from the age-dependent model (0.22, 95%CI= 0.20-0.23) was intermediate between \hat{M} predicted by the growth-dependent (0.20, 95%CI= 0.18-0.22) and temperature-dependent models (0.25, 95%CI= 0.23-0.28). I observed substantial differences between natural mortality rates (\hat{M}) estimated with all models and age-specific natural mortality rates (M_t) at young ages. Age-specific mortality (M_t) declined rapidly between ages one and five (Table 4.3). Annual mortality declined by less than 2% between subsequent ages after age five and by less than 1% after age eight.

Table 4.3.- Age-specific mortality rates (M_t) and 95% confidence limits (CL) for grass carp in Lake Gaston estimated using an age-dependent model of mortality. When mortality was averaged across all ages, $\widehat{M}= 0.22$.

Age	Mt	Upper 95% CL	Lower 95% CL
1	0.47	0.43	0.51
2	0.36	0.33	0.38
3	0.30	0.28	0.31
4	0.26	0.24	0.27
5	0.23	0.22	0.24
6	0.21	0.20	0.22
7	0.20	0.19	0.21
8	0.19	0.18	0.20
9	0.18	0.17	0.19
10	0.17	0.16	0.18
11	0.17	0.15	0.18
12	0.16	0.15	0.17
13	0.16	0.15	0.17
14	0.15	0.14	0.17
15	0.15	0.14	0.16
16	0.15	0.14	0.16
M	0.22	0.20	0.23

Despite apparent similarities in \widehat{M} predicted by all three models, I observed a wide range of estimated population sizes (Figure 4.2). Population sizes (\widehat{N}_i) estimated by the temperature-dependent model were intermediate to and significantly different from those estimated with the growth-dependent model (df=15, $t=-9.05$, $p<0.001$) and the age-dependent model (df=15, $t=-9.03$, $p<0.001$). Population sizes estimated from the growth-dependent and age-dependent models also differed significantly (df=15, $t=9.05$, $p<0.001$). Annual population sizes predicted with M_t in the age-dependent model were consistently smaller than those predicted by using \widehat{M} derived with growth- and temperature-dependent models. There was no significant relationship between grass carp population size in year i and hydrilla coverage in any year considered in time-lag scenarios (i.e., i , $i+1$, $i+2$, $i+3$).

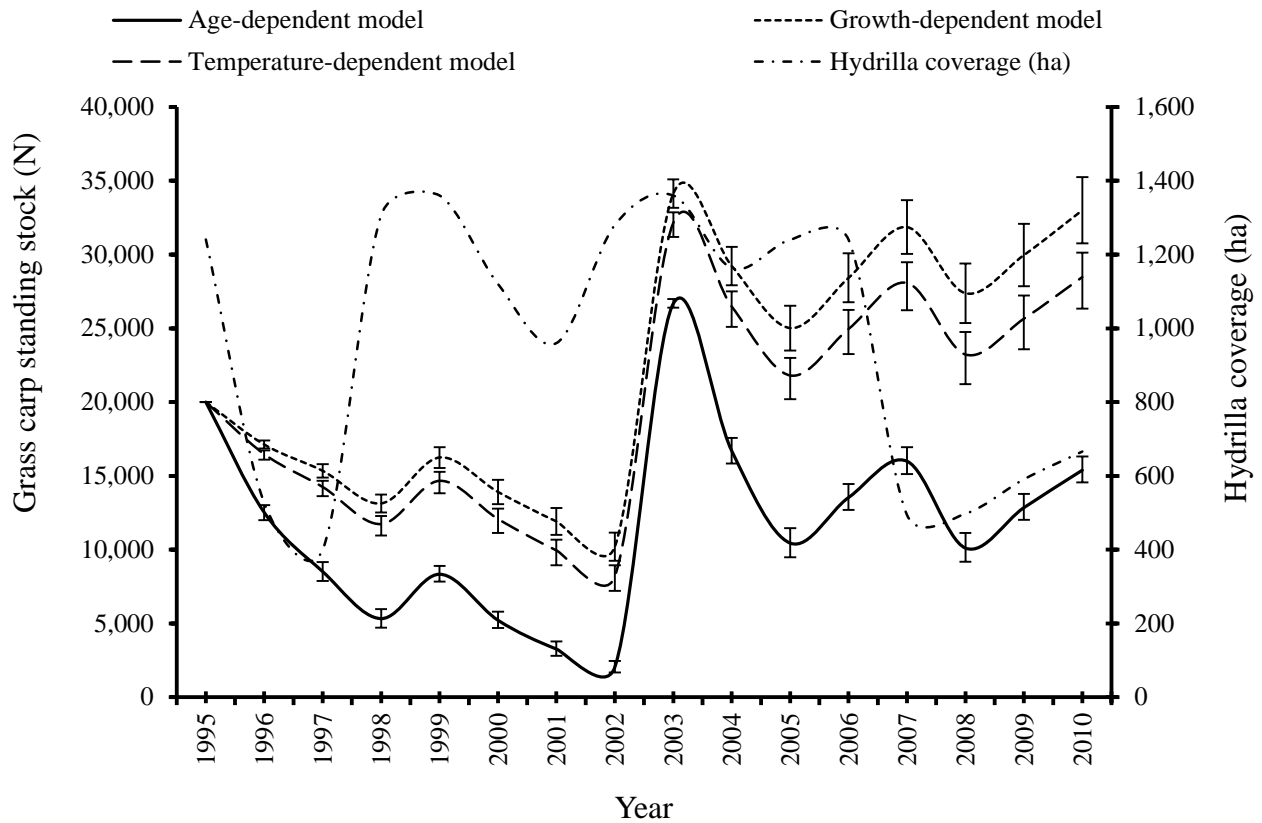


Figure 4.2.- Estimated grass carp population size (\pm 95% CI) in Lake Gaston 1995-2010.

Population size (\hat{N}_i) was predicted using \hat{M} for growth-dependent and temperature dependent models. Estimates of \hat{N}_i derived from the age-dependent model used M_t for each age (t).

Estimates of grass carp biomass 1995-2010 varied considerably depending on the model used (Figures 4.3-4.5). The growth-dependent model consistently predicted the greatest \hat{B}_i , and the age-dependent model the least. In years of greatest disparity between model estimates, biomass derived by the growth-dependent model was more than double that derived with the age-dependent model.

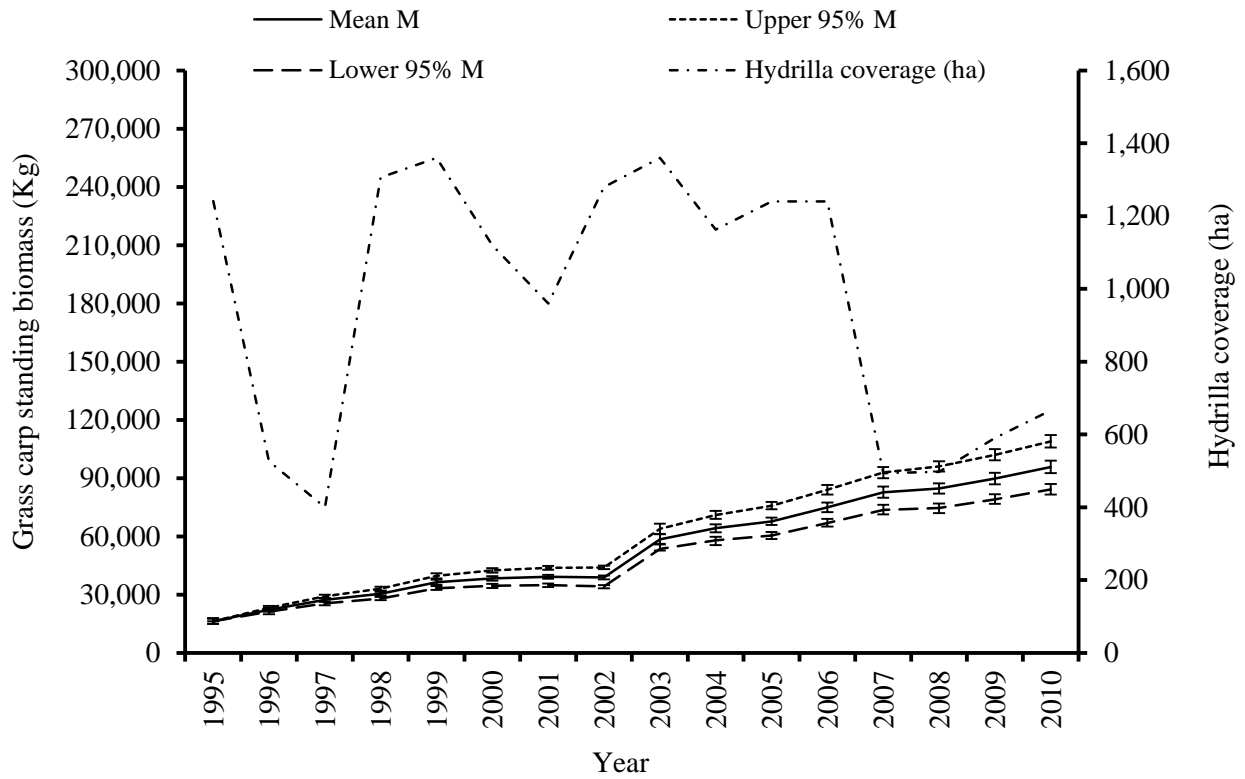


Figure 4.3.- Annual hydrilla coverage 1995-2010 compared to estimates of standing biomass of grass carp ($\pm 95\%$ CI) derived using the age-dependent model. Biomass was estimated using the mean and 95% confidence limits (CL) for mortality at each age (M_t), and the 95% CI around each biomass estimate is based on the 95% CL for weight at each age.

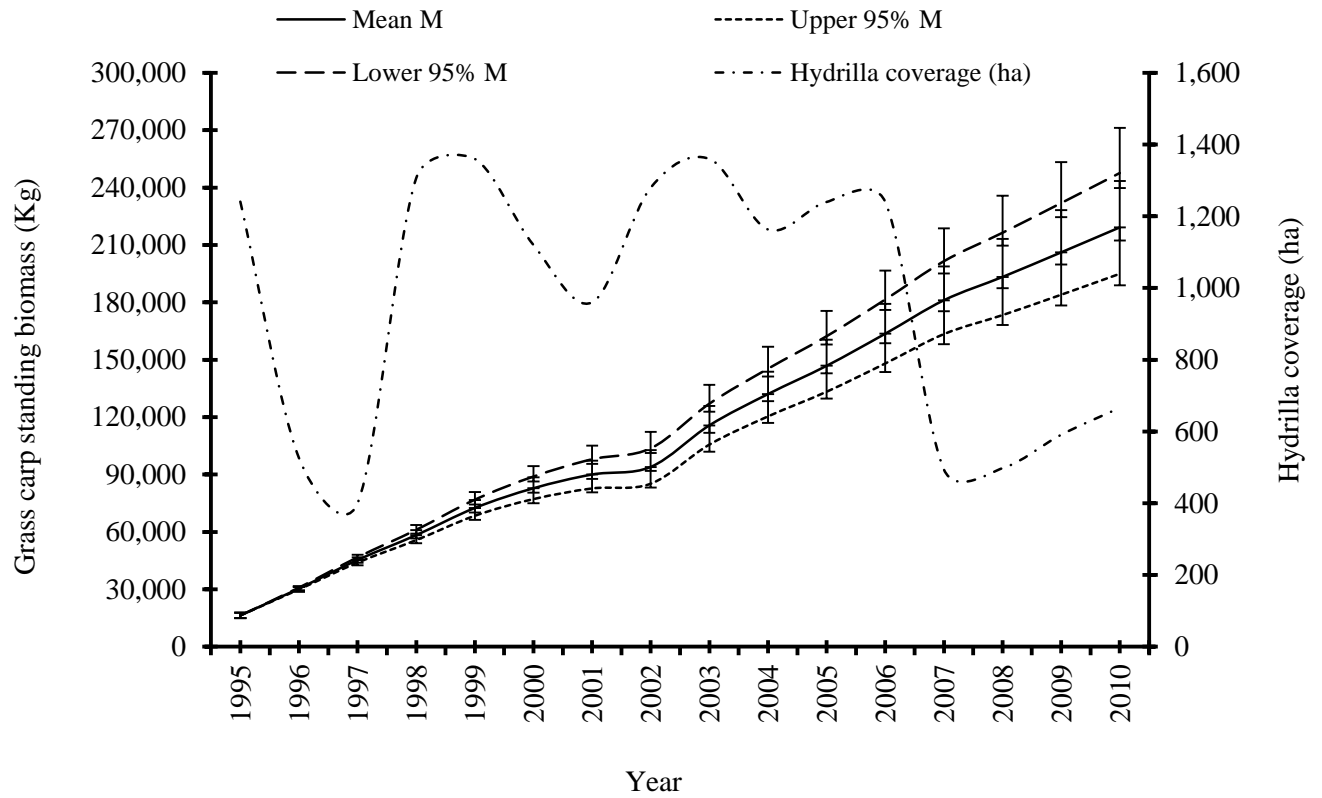


Figure 4.4.- Annual hydrilla coverage 1995-2010 compared to estimates of standing biomass of grass carp ($\pm 95\%$ CI) derived using the growth-dependent model. Biomass was estimated using the mean and 95% confidence limits (CL) for mortality at each age (M), and the 95% CI around each biomass estimate is based on the 95% CL for weight at each age.

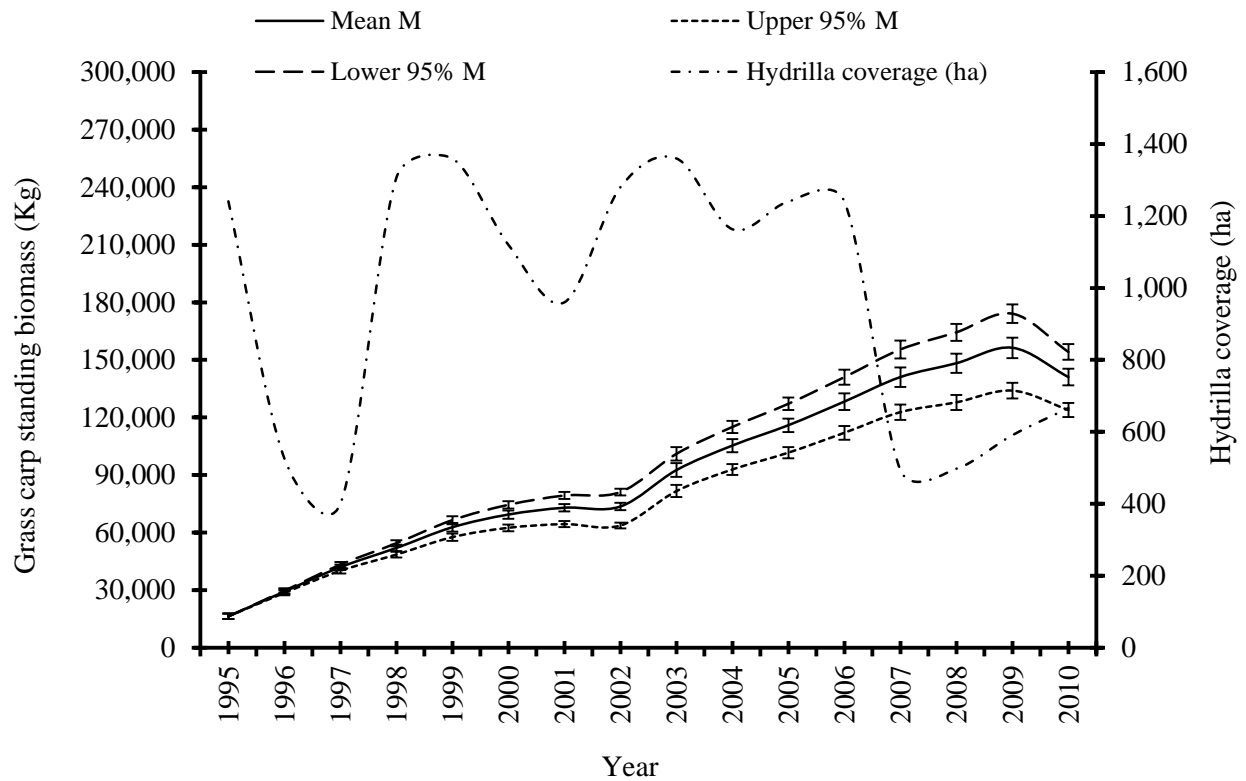


Figure 4.5.- Annual hydrilla coverage 1995-2010 compared to estimates of standing biomass of grass carp ($\pm 95\%$ CI) derived using the temperature-dependent model. Biomass was estimated using the mean and 95% confidence limits (CL) for mortality (M), and the 95% CI around each biomass estimate is based on the 95% CL for weight at each age.

A significant, negative relationship existed between grass carp biomass in time i and hydrilla coverage in year $i+3$ using all three mortality estimates (Figure 4.6). This means, for example, that the best prediction of hydrilla coverage in 1998 was grass carp biomass in 1995. The relationship between grass carp biomass and hydrilla coverage was not significant using any

other time-lag scenario. The regression statistics for each model are described in Table 3.

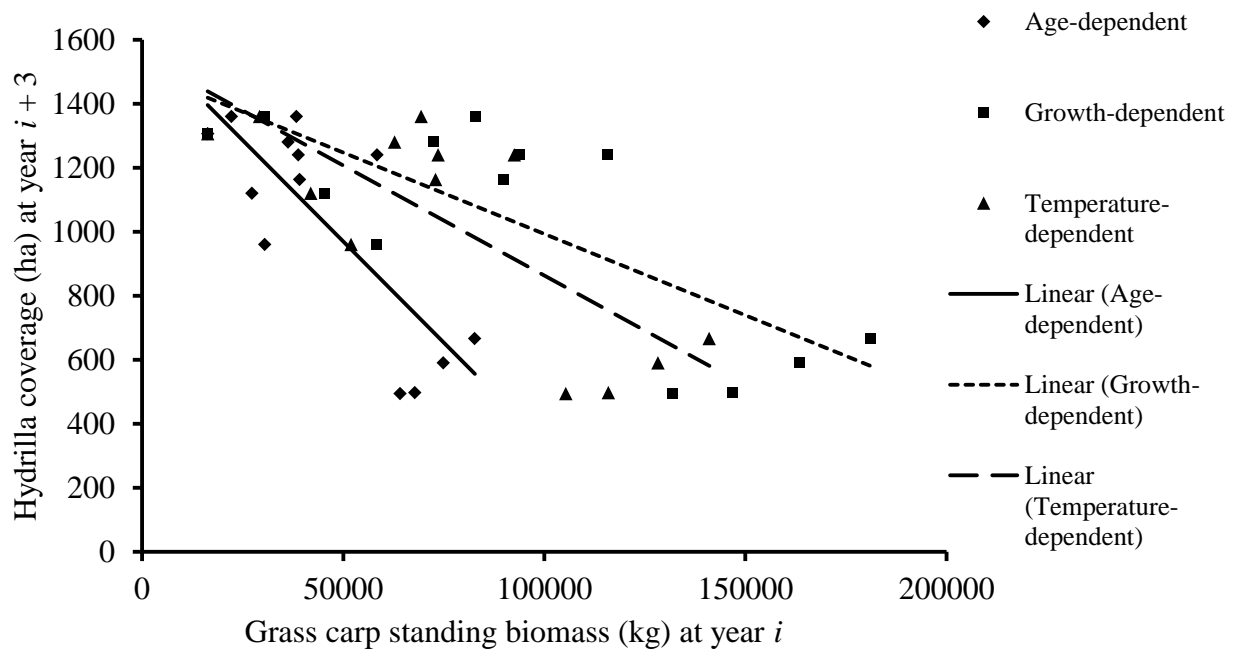


Figure 4.6.- Regressions describing the relationship between hydrilla coverage estimated at time $i+3$ and grass carp biomass estimated at time i with three methods.

The regression derived from annual biomass estimated with the age-dependent model provided the best fit for describing the relationship between grass carp biomass and hydrilla coverage. It had the second-lowest *PRESS*, lowest Mallow's *C_p*, and had the highest r^2 -adjusted value (Table 4.4). According to this model, I predicted that biomass needed to reduce hydrilla to 120 ha in Lake Gaston ($\pm 95\%$ prediction interval- PI) is about 91,184 kg ($\pm 38,146$ kg). The biomass of grass carp that would reduce hydrilla coverage to 0 ha (\pm PI) is 97,199 kg ($\pm 40,024$ kg). In 2010, grass carp biomass in Lake Gaston (\pm CI) reached 91,000 kg for the first time ($95,768 \pm 3203$ kg) (Figure 4.7). Based on age-specific mortality rates I estimate that, in 2011, the standing biomass of grass carp in Lake Gaston (\pm CI) will be about 108,073 kg ($\pm 3,609$ kg)

including the biomass of fish stocked in spring 2011. After 2011, biomass will decrease without further stocking.

Table 4.4.- Model-discrimination statistics for regressions describing the relationship between hydrilla coverage in time $i+3$ and biomass of grass carp in Lake Gaston in time i . Biomass was estimated by three different models.

Model	<i>Df</i>	r^2 -adjusted	Mallow's <i>Cp</i>	<i>PRESS</i>	<i>F</i>	<i>p</i>
Age-dependent	11	58.6	6.1	703497	17.97	0.001
Temperature-dependent	11	55.8	7.1	766407	16.13	0.002
Growth-dependent	11	57.6	6.4	697359	17.32	0.002

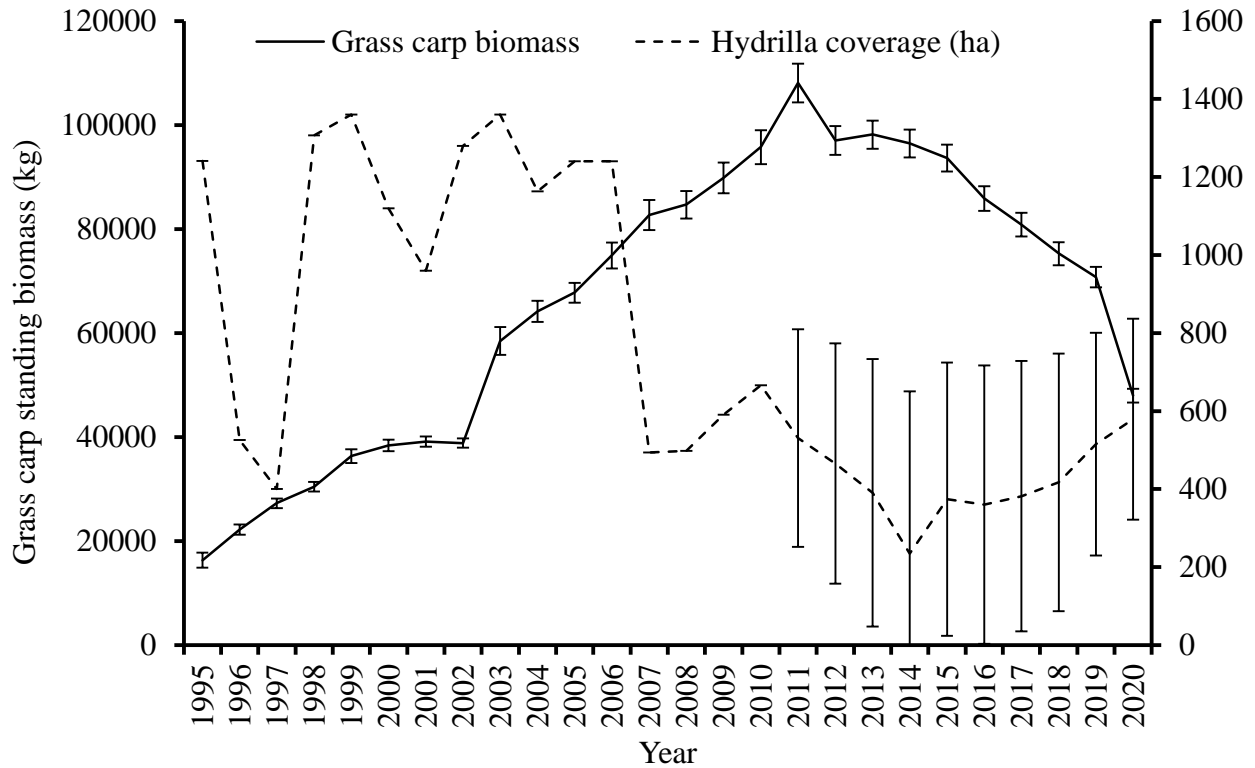


Figure 4.7.- Projections of grass carp standing biomass ($\pm 95\%$ CI) assuming no further stocking after 2011 and hydrilla coverage through 2020. Biomass predicted after 2011 was based on stable mortality through age 26 and linear growth in weight with age through age 26. Hydrilla coverage ($\pm PI$) was predicted after 2010 based on the relationship between grass carp standing biomass at year i and hydrilla coverage at year $i+3$. No estimate of error was available for hydrilla coverage prior to 2010.

Discussion

Previous studies have documented difficulties capturing grass carp for population analyses (Stott and Russell 1979; Bonar et al. 1993). In systems where grass carp are caught over a long period of time by volunteer bowfishers, the methods presented by Morrow et al. (1997) and expanded herein provide a cost-effective means for estimating important population

parameters. All estimates of natural mortality (\widehat{M}) in this study were within 5% of one another, despite differences in the models, suggesting that the three methods provide a reasonable level of precision. My estimates of natural mortality were also similar to the 22% annual mortality estimated by Morrow et al. (1997). Because of the similarities between estimates of natural mortality in this study and others, I speculate that my methods present a reliable alternative to catch-curve analysis when catch data from bowfishing violate underlying assumptions of equal catchability across year classes. Because von Bertalanffy parameters estimated by Morrow et al. (1997) were estimated for fish only through age 6, and Kirk et al. (2000) did not report parameter estimates, we have no meaningful way to compare estimates of mortality from their catch-curve analyses to indirect methods of estimation. The accuracy of indirect mortality estimates relies heavily on the accuracy of parameter estimation for the von Bertalanffy growth model. It is intuitive that data from long-lived, established populations of grass carp would yield more-reliable parameter estimates for the growth model. For such populations, our methods provide a useful technique for estimating mortality rates and associated population parameters.

The growth of grass carp in Lake Gaston appears to be different than growth of other documented populations. For example, the length-weight relationship described by the power function (Ricker 1975) indicates that grass carp in Lake Gaston become less rotund as they grow in length. This is contrary to the findings of Morrow et al. (1997), who indicated that grass carp become more rotund as they grow longer. Both in Lake Gaston and in the Santee-Cooper system (Morrow et al. 1997) weight was approximately linear with age. The results of Morrow et al. (1997) were based on a population of grass carp with a maximum age of 6 years and a theoretical length of 1,044 mm. In Lake Gaston, grass carp up to 16 years of age have been collected, and

the maximum length observed was 1,350 mm. These results indicate that grass carp may become more rotund with length to a certain point, and decrease in body condition thereafter.

It seems that using age-specific mortality to estimate population parameters is a more-cautious and, perhaps, more-realistic approach to grass carp management than using average, annual mortality estimates. Age-1 mortality estimated with the age-dependent model in this study was about 0.47. By comparison, the estimate of age-1 mortality resultant from the time-dependent telemetry model of age-1 grass carp mortality in Lake Gaston was $0.43(\pm 0.10)$ (chapter 2). There were clear differences in the estimated population size and biomass that resulted from the manner in which each model treated mortality at young ages in the present study. Despite differences between the models used to estimate mortality, the relationship between hydrilla coverage and estimated grass carp biomass is similar in all three models. The result is that the number of fish recommended for desired hydrilla control would be vastly different depending on the model used to estimate mortality. Use of age-dependent mortality resulted in the smallest estimates of standing biomass. Therefore, the difference between standing biomass and the biomass needed to reduce hydrilla to target levels is smaller using age-specific mortality because the scale of biomass is greatly reduced compared to the other two models. Thus, fewer fish are needed at stocking to reach target levels of grass carp biomass in a given year. As grass carp biomass nears the predicted weight necessary to reduce hydrilla coverage to the target level of 120 ha in Lake Gaston, the risk of not achieving an exact level of control is outweighed by the risk of overshooting target control. By stocking fewer fish at a given time, managers can decrease the risk of overshooting the target level of hydrilla control.

I observed a considerable lag period between fish stocking and detectable effects on hydrilla coverage. It appears that fish biomass in the fourth year after a major stocking event

may be a limiting factor in a cohort's capacity to control hydrilla effectively in Lake Gaston. My evaluation of growth rates in Lake Gaston indicated that growth (mm/yr) became asymptotic after age four. Age-specific mortality estimates indicated that mortality stabilized after age four. Grass carp biomass decreased in 1998, 2002, and 2006. These decreases indicate points in time when fish growth (kg/yr) was not able to compensate for losses in fish biomass due to mortality. As a result, the biomass of grass carp in the lake was not able to compensate for hydrilla growth in 1998, 2002, and 2006. Each of the decreases in estimated biomass occurred four years after a stocking event. These results suggest that the interaction between growth and mortality after age three was the most limiting factor to successful hydrilla control.

In Lake Gaston, there is a significant relationship between the biomass of fish and hydrilla coverage, but not the number of fish and hydrilla coverage. In past years, stocking rates of grass carp in Lake Gaston have been decided based on a target-number of fish per vegetated hectare. By using mortality rates and age-weight relationships developed in this study, the management team at Lake Gaston could, with reasonable precision, determine the biomass of fish required to attain a given level of hydrilla cover within three years of stocking. More-refined stocking models are available to produce estimated numbers of grass carp needed to control a given acreage of hydrilla over time (e.g. Stewart and Boyd 1999), but these models are useful only to about 10 years after stocking. In Lake Gaston fish older than 10 years may make substantial contributions to the total biomass, but not the number, of grass carp in the lake and so they must be considered in stocking models. Since weight gain of grass carp in Lake Gaston is approximately linear with age, there is reason to believe that old fish continue to provide control of aquatic weeds up to age 16, and should therefore be considered in stocking models. Based on

the results of this study, biomass may be a more-appropriate index of fish density, since no relationship was found between fish numbers and hydrilla coverage.

In 2003, grass carp biomass first reached the lower threshold of the prediction interval of biomass needed to reduce hydrilla coverage to 120 ha after fish biomass was increased by about 20,000 kg due to maintenance stocking of 25,000 fish. Grass carp biomass continued to increase from 2003-2010 due to more-frequent stocking that caused overlap in the biomass production resultant from consecutive age-classes. Based on the time lag observed in this study, I expect that the 2010 biomass of grass carp in Lake Gaston will reduce hydrilla coverage to 120 ha between 2013 and 2018. According to biomass estimated with age-specific mortality, it does not appear that the biomass of grass carp in Lake Gaston was high enough in 2009 to reduce hydrilla coverage to less than 120 ha by 2012. This estimate of grass carp biomass for 2011 indicated that no stocking was necessary in 2011 to maintain the target-level of hydrilla control through 2014. However, a total of approximately 13,400 fish were stocked in Lake Gaston in 2011 based on recommendations from models of fish per vegetated hectare. Given the timing and magnitude of the 2011 fish stocking, it is possible that hydrilla coverage in Lake Gaston could be reduced to zero ha in 2014. After this time, the likelihood of hydrilla eradication would be greatly reduced without further stocking.

The results of this study indicate that at current stocking levels, grass carp in Lake Gaston successfully control hydrilla without eradicating it, but have only recently reached a high-enough biomass to reduce hydrilla to 120 ha. While grass carp will not likely reduce hydrilla coverage to 120 ha by 2012, the target level of coverage should be achieved between 2013 and 2018 with no further grass carp stocking. Stocking more grass carp in 2012 could push hydrilla control beyond the target level of 120 ha and begin to affect the success of efforts to replant native

vegetation. The first year that grass carp stocking would be necessary in order to reduce hydrilla coverage back to target levels would be in 2019. A stocking of approximately 21,000 kg (± 1980 kg) would be needed to return the standing biomass of grass carp in Lake Gaston to the biomass necessary to reduce hydrilla to 120 ha. Based on the average weight of age-1 grass carp in Lake Gaston (.816 kg), about 25,000 fish would be recommended for stocking in 2019. In the future, stocking decisions at Lake Gaston should be based on maintaining target levels of grass carp biomass, rather than the number of fish per vegetated hectare.

Chapter 5: Summary and conclusion

Summary

Movements and habitat use of grass carp

The movements and habitat use of 101 radio-tagged grass carp were monitored for up to 2 years after tagging in 2007, 2008, 2009, and 2010. Tagged fish ranged 264-573 (mm,TL) in length and 466-9680 g in weight. Fish were tagged and stocked at three different sites in Lake Gaston, VA and NC. I related the movement rates, depth of water at fish location, and distance of grass carp from the nearest shoreline to variation in fish age, climate, reservoir operations, and where fish were stocked.

Grass carp behavior changed in Lake Gaston based on the age of fish. Grass carp moved more during their second year in the reservoir than in the first year. Although grass carp moved more, they were found closer to shore in their second year. This suggests that as grass carp age, they make more-extensive use of the habitat available in Lake Gaston.

Several climate variables were related to grass carp behavior. Water temperature was related to all aspects of grass carp behavior measured in this study. Grass carp moved the least when water temperature was low, and were found in the shallowest water. This relationship suggests that grass carp make more use of areas where hydrilla can grow during summer in Lake Gaston. My results also suggest that weather phenomena were also related to grass carp behavior. For example, when it was windy at Lake Gaston, grass carp moved more and were found further from shore.

Several measures of flow dynamics in Lake Gaston were related to grass carp behavior. For example, fish moved more and were located closer to shore when lake elevation was high.

But when outflow from Lake Gaston was high, fish moved more and were located in deeper water. These results illustrate relationships between grass carp behavior and reservoir-flow dynamics that warrant further investigation in future studies.

Finally, grass carp were found closer to shore in the upstream reaches of Lake Gaston than in the downstream reaches. These results are likely due to differences between ends of the reservoir such as habitat availability, flow regime, food availability and human uses. In Lake Gaston, the upper reservoir is dominated by creeks and flats suitable for hydrilla growth, and sees comparatively less human use than the lower reservoir, which is dominated by open water and main-channel habitat. The implication of this finding is that grass carp may make better use of areas targeted for hydrilla control in the upper reservoir. Thus, management could benefit from knowledge of how other aspects of the grass carp population change from one end of the reservoir to the other.

Variation in age-1 survival of grass carp

I used location data from 40 grass carp that were radio tagged in 2009 to estimate age-1 survival of grass carp in Lake Gaston. I used capture-mark-recapture models developed for use in radio-tagged animal populations to characterize variability in age-1 survival due to factors under the control of management. Specifically, I investigated the plausibility that survival might be influenced by stocking location, fish size at stocking (length and weight), fish condition at stocking, and tagging methods.

I found that the most-plausible model of age-1 grass carp survival was that which allowed survival to vary throughout the year. This model suggested that probability of grass carp surviving the first year after stocking was $0.57(\pm 0.10)$. The second-most-likely model among the

set tested in this study was that which allowed survival to vary by stocking location. This model suggested that survival in the upper reservoir $0.87(\pm 0.09)$ was more than double that in the lower reservoir, $0.43(\pm 0.11)$.

None of the models that allowed survival to vary due to grass carp size or condition displayed a meaningful level of support among the models tested. Because grass carp as long as 573 mm were included in this study, I speculate that fish of any size from this study were large enough to minimize increases in predation due to size. Therefore, I recommend that the minimum size used in this study (352 mm, TL) is sufficient as a minimum size for stocking in Lake Gaston. This length is nearly 100 mm shorter than the minimum size of 450 mm recommended elsewhere in literature.

The results of this study, in conjunction with knowledge of grass carp behavior in Lake Gaston, imply that the cost-effectiveness of grass carp stocking could be improved upon over current practices. For example, grass carp appear to be more closely associated with shoreline habitat in the upper reservoir, and grass carp survival through the first year after stocking is nearly twice as high in the upper reservoir than in the lower reservoir. Furthermore, grass carp that were stocked in the upper reservoir were found to move throughout the lake in their second year. These results suggest that the cost of grass carp stocking could be reduced by stocking grass carp in the upper reservoir, and that effectiveness of stocking would be increased due to greater use of target areas by fish during their first year. The cost of stocking grass carp in Lake Gaston could be further reduced by using a minimum size of 352 mm instead of the minimum size of 450 mm currently in use. By using a smaller size, managers would reduce the amount of time that grass carp were held at fish culture stations, and therefore the cost of production. The result is that smaller fish cost less to stock.

Growth and population dynamics of grass carp

A total of 243 grass carp were collected by specially permitted bowfishers for research about the growth and population dynamics of grass carp in Lake Gaston. Fish collected by bowfishers were 410-1350 mm (TL) and 450-34019 g. The ages of individual grass carp were determined from lapili otoliths, and a growth history was constructed for each fish by relating the size of grass carp to growth increments in the otoliths. I estimated von Bertalanffy growth parameters for the Lake Gaston grass carp population using information on length at age from fish measurements at capture, as well as back-calculated growth-histories. I used the growth parameters to estimate instantaneous mortality of grass carp in Lake Gaston with three different methods that based mortality on growth, temperature, and age. Using mortality estimates resultant from each method, I estimated the population size and the standing biomass of grass carp in Lake Gaston 1995-2011. I compared these estimates to hydrilla coverage in the lake over the same time period to determine relationships between grass carp population dynamics and hydrilla coverage.

Grass carp collected in this study were 1-16 year of age. I found that grass carp growth (mm/yr) slowed with increasing age, and that the difference in growth between consecutive ages was not significant after age four. Grass carp weight (g) was approximately linear with age, although fish became less rotund with age. The results of the growth analysis suggest that grass carp continue to grow in both length and weight through older ages.

I found that grass carp mortality estimated from the three different methods used in this study led to divergent estimates of population size and standing biomass. Estimates of instantaneous mortality ranged from 0.20 to 0.25 depending on the method used. Age-specific

mortality of grass carp decreased from 0.47 at age one to 0.15 at age 16. Mortality decreased less than three percent between consecutive ages and by less than one percent after age eight.

There was a significant relationship between the biomass of grass carp in Lake Gaston at year i and surface hectares of hydrilla in the lake at year $i+3$. These results suggest that there is a time lag between grass carp stocking and noticeable effects on hydrilla. This lag is likely due to changes in the size structure of the population after age four, in conjunction with changes in survival after age four. After age four, growth (kg/yr) is not able to compensate for losses in standing biomass due to mortality. I was not able to identify any significant relationships between grass carp numbers and hydrilla coverage in any time after stocking, suggesting that interactions between growth and mortality at young ages are more important to determining subsequent effects on hydrilla than changes in mortality alone.

This study provides information regarding long-lived grass carp incrementally stocked for hydrilla control. Most studies of grass carp are of populations that eradicate submerged vegetation in only a few years and senesce due to lack of food resources. The information generated in this study is of immediate utility to the weed-management team at Lake Gaston. Using this information, I was able to predict the biomass of grass carp necessary to reduce hydrilla coverage to target levels, in what time frame control should be achieved, and what the potential effects of stocking might be.

Conclusion

The research conducted in this study should be useful for informing management of long-lived grass carp populations used in weed control. I was able to illustrate relationships between grass carp behavior and factors such as age, stocking location, climate, and hydrodynamic

processes. I identified needs for future research regarding the effects of flow on behavior and other environmental conditions. The post-stocking survival estimates from chapter two will be useful for guiding management decisions such as the minimum size for grass carp at stocking, and where to stock them. Finally, information developed in this study regarding growth and population dynamics of grass carp will be useful for guiding stocking decisions at Gaston and similar systems.

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