Growth and Population Size of Grass Carp Incrementally Stocked for Hydrilla Control

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Abstract

    In weed control plans that use Grass Carp *Ctenopharyngodon idella* for intermediate control of hydrilla *Hydrilla verticillata*, the knowledge of population dynamics improves efficacy of management. Our objective was to characterize growth, mortality, and associated population metrics of long-lived (up to 16 years) triploid Grass Carp that were incrementally stocked into Lake Gaston, Virginia–North Carolina, starting in 1995. Grass Carp (ages 1–16) were collected by bowfishers during 2006–2010. Growth of Grass Carp was described by the von Bertalanffy growth model as $L_t = 1,297[1 - e^{-0.1352(t + 1.52)}]$, where L_t is TL at age t. We used three methods to estimate Grass Carp mortality, and annual abundance and biomass of Grass Carp were estimated from each mortality estimate. Estimated annual mortality ranged from 0.20 to 0.25 depending on the method used. The use of constant mortality rates versus age-specific mortality rates produced divergent models of Grass Carp biomass and represented a different approach for tracking the progress of weed control. Grass Carp biomass (but not abundance) was related to hydrilla coverage in Lake Gaston based on several scenarios that described time lags between Grass Carp stocking in year i and decreases in hydrilla coverage (in years $i, i + 1, \ldots, i + 5$). Regardless of the mortality estimate used to derive Grass Carp biomass, the strongest biomass–hydrilla coverage relationship was observed for a time lag of 4 years. Fish older than age 10 constituted nearly 50% of the total Grass Carp biomass in Lake Gaston during some years, and the relationship between Grass Carp biomass and hydrilla coverage was strongest when fish up to age 16 were included in models. These results indicate that Grass Carp up to at least age 16 are important for weed control, thus highlighting the need for stocking models and bioenergetics models that include contributions of older fish when assessing long-lived Grass Carp populations.

Grass Carp *Ctenopharyngodon idella* have been widely stocked for biological control of aquatic vegetation in the USA since the species' introduction in 1963 (Mitchell and Kelly 2006). The Grass Carp has been proven as an effective control agent for invasive aquatic weeds, including hydrilla *Hydrilla*

verticillata, which is a preferred food source for Grass Carp (Allen and Wattendorf 1987; Chilton and Muoneke 1992; Kirk et al. 2000). However, variable success has resulted in Grass Carp stocking rates that range from 2 to 500 fish/vegetated hectare (Kilgen and Smitherman 1971; Allen and Wattendorf

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1987; Bonar et al. 1993, 2002; Kirk et al. 2000). Traditional approaches to using Grass Carp for biological control of hydrilla often involve large, isolated stocking events. 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 (including nontarget species) from aquatic systems (Stott and Robson 1970; Bettoli et al. 1993; Killgore et al. 1998; Schramm and Brice 2000).

In some cases, weed management goals target some intermediate level of noxious weed infestation that is specific to stakeholder views and generally is based on some predetermined surface coverage of hydrilla (Bonar et al. 2002). This management goal is highly controversial but generally is the result of conflicting stakeholder views (Chilton and Magnelia 2008; Richardson 2008). One approach to the intermediate control of hydrilla is the incremental stocking of Grass Carp in combination with low-level herbicide application (Chilton and Magnelia 2008; Chilton et al. 2008). This approach theoretically allows fisheries managers to make adjustments to Grass Carp stocking rates so that fish density can be maintained at a desired level based on knowledge of the population's growth, mortality, and longevity. However, information regarding population characteristics of Grass Carp is often lacking; therefore, stocking rates are commonly determined on the basis of maintaining a desired number of Grass Carp per total surface area of the lake or per unit of surface weed coverage (e.g., Kirk et al. 2000; Bonar et al. 2002; Chilton and Magnelia 2008; Chilton et al. 2008) rather than based on the biology of Grass Carp in the system of interest. For example, this management approach assumes that for the purpose of making management decisions, the number of Grass Carp in a system is more important than Grass Carp biomass; however, this assumption has not been validated for large reservoirs.

Mortality and growth rates of Grass Carp vary by geography, climate, availability of food, and fish age (Chilton and Muoneke 1992). State and federal agencies have developed software programs that predict, based on a host of factors, the potential effects of a cohort for up to 10 years after stocking (e.g., Stewart and Boyd 1999). Limiting the analyzed effects to 10 years poststocking is likely due to the contention in the published literature that triploid Grass Carp older than age 10 make up a negligible proportion of population size and biomass in most systems (Kirk and Socha 2003). However, we suspect that this belief results from (1) high stocking rates and subsequently high mortality rates of Grass Carp due to the elimination of aquatic vegetation in the system that received the stocked fish (e.g., Morrow et al. 1997; Kirk et al. 2000; Kirk and Socha 2003); (2) the application of assumed mortality rates in lieu of either indirect or direct estimation of Grass Carp mortality (e.g., Chilton and Magnelia 2008); and (3) the fact that Grass Carp are thought to consume less hydrilla and grow more slowly in proportion to body mass as they increase in body size and age (Gorbach 1961; Osborne and Sassic 1981).

Research has shown that Grass Carp may live up to 21 years in systems where food is plentiful (Gorbach 1961) and that growth

(in mass) of Grass Carp can be approximately linear with age (Gasaway 1978; Morrow et al. 1997). Although some life history studies have been conducted on triploid (sterile) Grass Carp (e.g., Morrow et al. 1997; Kirk et al. 2000), little information exists regarding the characteristics of established populations that have not eradicated all of the vegetation in the stocked water body. As integrated pest management (IPM) becomes more common as an approach to aquatic weed control (Chilton and Magnelia 2008; Richardson 2008), knowledge of the population dynamics of long-lived, incrementally stocked Grass Carp populations will become increasingly important because the IPM approach relies more on long-term, low-level Grass Carp stocking than on traditional stocking strategies, which are designed to eradicate vegetation in the short term.

Hydrilla was first identified in Lake Gaston, Virginia–North Carolina, in 1992 (Ryan et al. 1995). Since then, millions of dollars have been spent on hydrilla control in the reservoir. Coverage of hydrilla was initially about 10 ha and later peaked at 1,364 ha in 2003 (Dodd-Williams et al. 2008). Since 1995, incremental Grass Carp stocking has been integrated with annual fluridone applications to control hydrilla in Lake Gaston (Lake Gaston Weed Control Council [LGWCC], unpublished; www.lgwcc.org). The hydrilla leaf-mining flies *Hydrellia pakistanae* and *H. balciunasi* (Diptera: Ephydridae) were introduced into the lake in 2004, but they failed to establish viable populations and are considered to have been ineffective (Grodowitz et al. 2010). Due to the highly controversial nature of aquatic weed control (Kirk and Henderson 2006) and the variety of conflicting views among Lake Gaston stakeholders (see Richardson 2008), the goal of weed control at the lake is not the complete eradication of hydrilla. Instead, the management goal for hydrilla control, as established by the LGWCC, is "to develop and maintain a healthy lake ecosystem based on a diverse plant community dominated by native species" (LGSB 2005:8). To achieve this goal, one stated objective of management is to reduce hydrilla coverage to 120 ha by 2012. The remaining hydrilla coverage of 120 ha is designed to serve as a buffer for expected Grass Carp grazing and to allow for the re-establishment of desirable aquatic vegetation (LGSB 2005). The target density for Grass Carp standing stock in 2011 was 37 fish/vegetated hectare (LGWCC, unpublished; www.lgwcc.org). By 2010, hydrilla coverage in Lake Gaston was reduced to approximately 666 ha (ReMetrix 2011), but this level of coverage was unsatisfactory in relation to management objectives for the lake.

The present study is the result of research that began in 2006 to assess the current status of Grass Carp with regard to the efficacy of weed control in Lake Gaston. One objective was to characterize the growth and mortality of the long-lived Grass Carp population in Lake Gaston in order to estimate the current standing stock of Grass Carp in the lake. The second objective was to use the standing stock estimates to characterize relationships between hydrilla coverage and Grass Carp numbers and biomass in Lake Gaston. Our third objective was to explore the importance of Grass Carp up to age 16 for weed control and

to rank the relative contributions of various age-groups to the efficacy of weed control. The information and relationships defined in this study will be useful for assessing the current status of hydrilla control in Lake Gaston and should provide a basis for improved management through a better understanding of the Grass Carp's contribution to this long-term integrated weed management effort.

METHODS

Study site.—Lake Gaston is an impoundment of the Roanoke River and spans five counties in Virginia and North Carolina. The total surface area of the reservoir is 8,423 ha, the total volume is about 5.6×10^{11} L flowing at 1,245 m³/s, and the retention time is 29 d at the full-pond elevation of 61 m (Richardson 2008; Dominion Power 2010). The reservoir is bordered upstream by Kerr Reservoir and downstream by Roanoke Rapids Lake. Lake Gaston is operated to regulate discharges from Kerr Reservoir, the primary flood control station for the Lower Roanoke River; therefore, lake elevation fluctuates little in Lake Gaston, although flow is variable. The primary purpose of Lake Gaston is hydropower production, but it also supports popular sport fisheries and is a center of residential development in the region and therefore is used for a number of non-consumptive recreational activities (Richardson 2008). Human population density is highest at the lower end of the reservoir, whereas the upper portion of the reservoir is sparsely populated and includes designated wildlife management areas. The reservoir also acts as a major source of drinking water for the City of Virginia Beach (Cox 2007).

Age and growth.—Specially permitted volunteer bowfishers collected 243 Grass Carp from Lake Gaston during 2006–2010. We measured TL (mm) and mass (g) of individual Grass Carp. Lapillar otoliths were removed from the fish and were prepared and aged by using methods that were documented in the literature but adapted based on technological advances (Morrow and Kirk 1995; Morrow et al. 1997). A consensus was reached between multiple readers in order to assign an age to each Grass Carp based on annular ring formation in otoliths.

The Fraser–Lee method was used to back-calculate lengths at each age (DeVries and Frie 1996). We estimated von Bertalanffy growth parameters (von Bertalanffy 1938) simultaneously from raw age–length data and plotted the von Bertalanffy growth curve in R software (R Development Core Team 2011). To optimize the fit of the von Bertalanffy growth model (VBGM), preliminary values of parameter estimates (obtained by using mean length at age in FAST; Slipke and Maceina 2001) were employed as starting values for the final parameter estimation in R. Parameter estimates for the growth curve were reported in the following form:

$$L_t = L_\infty[1 - e^{-K(t-t_0)}], \tag{1}$$

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 the Brody growth coefficient, and t_0 is the arbitrary origin of the equation (i.e., theoretical age at zero length; von Bertalanffy 1938). We estimated 95% confidence intervals (CIs) for growth parameters by using bootstrap methods iterated 20,000 times. We predicted mean length at age, and we constructed 95% CIs for lengths at each age by using the bootstrapped results for VBGM parameter estimates in R.

The length–weight relationship for Grass Carp collected from Lake Gaston was estimated by use of the function $W = a\text{TL}^b$, where a and b are constants, W is fish weight in grams, and TL is total length in millimeters (Ricker 1975). We used this equation to predict the weight of Grass Carp at each age from back-calculated lengths at age (Anderson and Neumann 1996). The predicted weight at each age was used in combination with mortality estimates (as described below) to estimate the biomass of Grass Carp in Lake Gaston.

Mortality.—Morrow et al. (1997) used bowfishing catch data to estimate Grass Carp mortality in the Santee–Cooper Reservoir system, South Carolina, by using catch curves. However, our data did not meet the assumptions of catch-curve analysis; therefore, we used three alternatives based on VBGM parameters. We used multiple methods to estimate mortality because (1) it is the only estimated demographic parameter used in predicting Grass Carp population size in Lake Gaston and (2) there is a high degree of uncertainty associated with using indirect methods of mortality estimation (Hewitt and Hoenig 2005). The first method we used was based solely on life history theory (Jensen 1996), the second method was based on empirical equations derived from meta-analysis of fish life history characteristics (Pauly 1980), and the third method was one that allowed age-specific mortality to be estimated based on fish life history characteristics (Chen and Watanabe 1989). We estimated 95% CIs for each of the three mortality estimates by using bootstrapped 95% confidence limits (CLs) for the VBGM parameters. To assess the importance of using growth parameters from an established population when using indirect estimates of mortality, we also estimated mortality from the VBGM parameters reported by Morrow et al. (1997) for Grass Carp in the Santee–Cooper Reservoir system. Because harvest of Grass Carp is not permitted in Lake Gaston, estimated annual natural mortality (M) represents the total annual mortality rate, and changes in the size of the Grass Carp population depend entirely on mortality (i.e., reproduction is zero due to triploidy).

Jensen (1996) demonstrated that the relationship between M and the growth coefficient K could be expressed as

$$\hat{M} = 1.50K. \tag{2}$$

Mortality rates that we estimated by using the method of Jensen (1996) will be referred to as $\hat{M}_j$.

Pauly (1980) estimated fish mortality based on relationships between L_∞, K, temperature (T), and M for 175 fish stocks as

$$\log_e \hat{M} = 0.654 \cdot \log_e K - 0.28 \cdot \log_e L_\infty + 0.463 \cdot \log_e T. \quad (3)$$

Temperature used for estimating mortality with this method can be based on average annual water temperature or on air temperature. We used average annual water temperature at Lake Gaston as measured in Grass Carp telemetry studies (D. S. Stich, unpublished data) that were conducted during the same years as the present study. Mortality estimates resulting from the Pauly (1980) method will be referred to as $\hat{M}_p$.

Finally, we used a method developed by Chen and Watanabe (1989) to estimate age-specific mortality rates (M_{cw}) of Grass Carp in Lake Gaston based on maximum observed age (t_{max}), K, and t_0 as described mathematically by

$$M_{cw} = \begin{cases} \dfrac{K}{1 - e^{-K(t-t_0)}}, t < t_{max} \\ \dfrac{K}{a_0 + a_1\,(t - t_{max}) + a_2\,(t - t_{max})^2}, t \geq t_{max} \end{cases} , \quad (4)$$

where a_0, a_1, and a_2 are constants pertaining to senescence.

Population size and biomass.—We used the $\hat{M}_j$ and $\hat{M}_p$ values to estimate the number of Grass Carp at each age remaining in Lake Gaston at the start of each year ($N_{t,i}$) based on the number of fish stocked (R_i) at time i:

$$N_{t,i} = N_{t-1,i-1} e^{(-\hat{M})} + R_{t,i}. \quad (5)$$

We also used age-specific estimates of mortality (M_{cw}) to estimate the number of Grass Carp in Lake Gaston at each age from 1995 to 2010 ($N_{t,i}$):

$$N_{t,i} = N_{t-1,i-1} e^{(-M_{cw})} + R_{t,i}. \quad (6)$$

We estimated population size at the start of each year ($\hat{N}_i$) and the biomass of Grass Carp in each age-class at the start of each year ($B_{t,i}$) by using each method of mortality estimation:

$$\hat{N}_i = \sum N_{t,i} \quad (7)$$

and

$$B_{t,i} = N_{t,i} W_t. \quad (8)$$

Finally, we estimated standing biomass ($\hat{B}_i$) of Grass Carp in Lake Gaston at the start of each year:

$$\hat{B}_i = \sum B_{t,i}. \quad (9)$$

We estimated the 95% CI for population size based on the 95% CLs for each mortality estimate; the 95% CI for biomass was estimated by propagating errors around estimated population size and weight at each age (Frishman 1975). For comparison with biomass estimated by using mortality derived from catch-curve analyses in other systems, we used mortality estimates reported by Kirk and Socha (2003; Santee–Cooper Reservoir system) to project biomass of the Lake Gaston Grass Carp population, and we developed 95% CIs for biomass based on weight at age in Lake Gaston.

Hydrilla coverage estimates used in this study were privately contracted by the LGWCC on an annual basis during 1995–2010. Because a time lag was expected to occur between Grass Carp stocking and subsequent effects on hydrilla coverage, we tested the relationship between model-estimated numbers and standing biomass of Grass Carp in year i and hydrilla coverage in years i, $i + 1$, $i + 2$, $i + 3$, $i + 4$, and $i + 5$ by using simple linear regression (Montgomery et al. 2006). Models of each time lag were ranked by using an information-theoretic approach based on Akaike's information criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002) in SYSTAT version 12 (SYSTAT 2007). When each model was fitted individually with the complete data set, all lag scenarios (including a lag of zero) indicated a strong empirical relationship between total Grass Carp biomass and hydrilla coverage ($R^2 > 0.90$). However, use of AIC_c to rank competing models requires that all models be drawn from the same set of observations (Burnham and Anderson 2002). To meet this requirement, only 1998–2005 data could be used for ranking the relative plausibility of different lags because (1) hydrilla data for 1996 and 1997 were not available and (2) the longest lag scenario (5 years) prevented us from including years after 2005.

We used the zero-lag model of the Grass Carp–hydrilla relationship to determine the importance of Grass Carp up to age 16 for controlling hydrilla in Lake Gaston. To accomplish this, we developed four additive models within a hierarchical framework to test the relative contributions of four Grass Carp age-groups (ages 1–4, 5–8, 9–12, and 13–16) to the efficacy of hydrilla control in Lake Gaston (Table 1). The use of these age-groups was intended to avoid overparameterization of models for age-classes in which data were sparse; however, the age-groups also coincide with previously documented changes in Grass Carp growth and mortality. For example, Grass Carp growth has been reported to be most rapid during ages 1–4 and declines to approximately 2.5 cm/year by age 8 (Gorbach 1961). The maximum age of Grass Carp in the southeastern USA was reported as 12 years (Kirk and Socha 2003), and the growth dynamics of Grass Carp older than age 12 are relatively undocumented in the USA. Because the existence of subsequent age-classes is dependent upon the existence of preceding age-classes, we did not construct reduced-parameter models that considered only the effects of the three oldest age-groups. The zero-lag scenario was used to maximize the data available for model subsets and

TABLE 1. Model development and description for additive models used to test the relative contributions of four age-groups of Grass Carp to the efficacy of hydrilla control in Lake Gaston, Virginia–North Carolina.

Model	Description
Hydrilla (B_4[a])	Response of hydrilla to biomass of Grass Carp ages 1–4
Hydrilla ($B_4 + B_8$[b])	Response of hydrilla to biomass of Grass Carp ages 1–8
Hydrilla ($B_4 + B_8 + B_{12}$[c])	Response of hydrilla to biomass of Grass Carp ages 1–12
Hydrilla ($B_4 + B_8 + B_{12} + B_{16}$[d])	Response of hydrilla to biomass of Grass Carp ages 1–16

[a]Biomass of Grass Carp ages 1–4.
[b]Biomass of Grass Carp ages 5–8.
[c]Biomass of Grass Carp ages 9–12.
[d]Biomass of Grass Carp ages 13–16.

because it allowed us to compare the relative weights of models that included the oldest fish present in the system, whereas long (e.g., 4- or 5-year) time lags would not. The information-theoretic approach based on AIC_c (in SYSTAT version 12) was used for model selection, and the relative plausibility of models was ranked based on AIC_c weights.

RESULTS

Growth and Mortality

Grass Carp ranged in age from 1 to 16 years, and all stocked cohorts except 2010 were represented in the sample (Table 2). The TL of Grass Carp ranged from 417 to 1,350 mm, and mass ranged from 0.95 to 34.0 kg. Grass Carp growth in Lake Gaston was highly variable within age-classes. The relationship between TL (mm) and weight (W; g) of Grass Carp was $W = (3.25 \times 10^{-5}) \times TL^{2.87}$ (Figure 1b), suggesting that Grass Carp became less rotund as TL increased (see Anderson and Neumann 1996). The relationship between weight (W_t; g) and

TABLE 2. Stocking years, number of fish stocked (N), and annual catch of Grass Carp by bowfishers in Lake Gaston, 2006–2010.

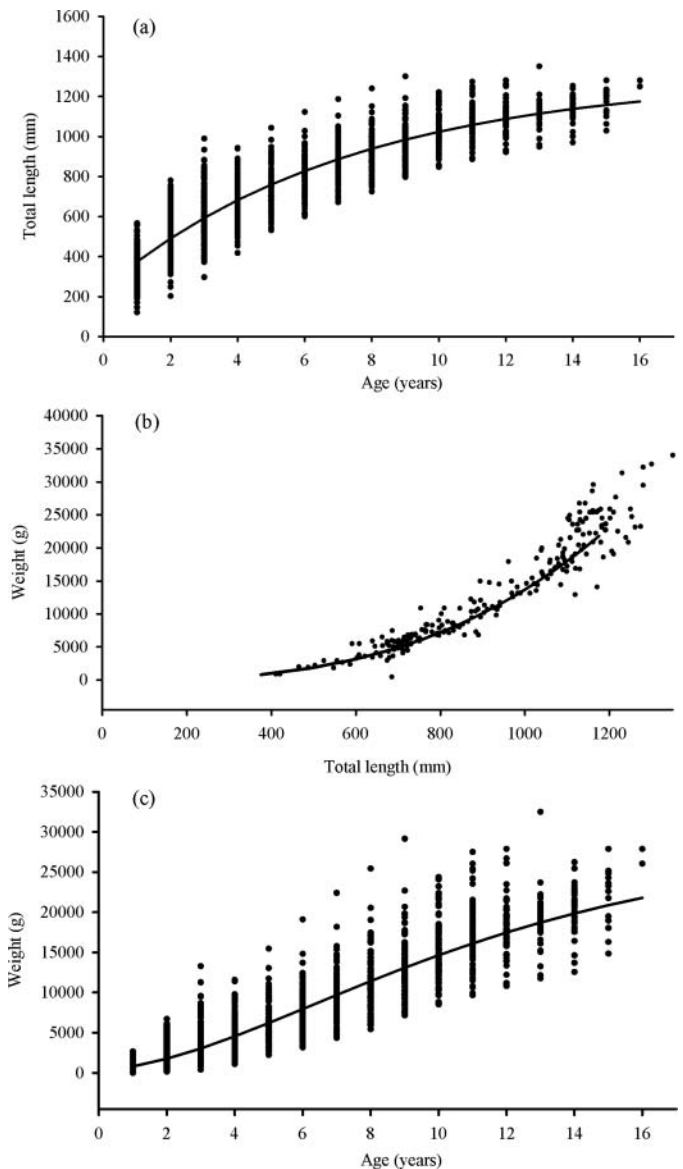| Cohort	N	Number caught per year					Total
		2006	2007	2008	2009	2010	
1995	20,000	12	25	9	17	22	85
1997	680	2	1	5	2	5	15
1999	5,000	0	2	1	3	12	18
2003	25,392	22	14	4	6	7	53
2006	7,000	1	7	7	16	9	40
2007	7,720	0	0	0	7	14	21
2008	100	0	0	0	0	9	9
2009	6,520	0	0	0	0	2	2
2010	7,347	0	0	0	0	0	0
Total	79,759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

FIGURE 1. Growth characteristics of Grass Carp in Lake Gaston, including **(a)** the von Bertalanffy growth model describing length at age, **(b)** the length–weight relationship, and **(c)** the age–weight relationship.

age t was nearly linear: $W_t = 1,448 + 1,623t$ ($r^2 = 0.99$, $P < 0.001$; Figure 1c). Predicted Grass Carp TL (mm) at each age was described by the VBGM as $L_t = 1,297[1 - e^{-0.135(t + 1.52)}]$, where L_t is length at age t (Figure 1a; Table 3).

The estimate of $\hat{M}_j$ (mean $= 0.20$; 95% CI $= 0.18$–0.22) was significantly different from the estimate of $\hat{M}_p$ (mean $= 0.25$; 95% CI $= 0.23$–0.28) within years (after 1996) based on the lack of overlap between 95% CIs. Age-specific mortality (M_{cw}) declined rapidly between ages 1 and 5 and declined by less than 2% between subsequent ages after age 5 and by less than 1% between ages after age 8 (Table 4). Although this pattern is expected based on the formulation by Chen and Watanabe (1989),

TABLE 3.   Means, SEs, 95% confidence limits (CLs), and test statistics for parameterization of the von Bertalanffy growth function used to describe growth of Grass Carp collected from Lake Gaston (L_∞ = asymptotic length [TL, mm]; K = Brody growth coefficient; t_0 = theoretical age at zero length).

Parameter	Estimate	SE	Lower 95% CL	Upper 95% CL	t	$P > t$
L_∞	1,297	24.160	1,253	1,348	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

the rate of decline in mortality between ages is a function of the specific growth characteristics of Grass Carp in Lake Gaston. When VBGM parameters from the Santee–Cooper Reservoir population (Morrow et al. 1997) were used to estimate mortality via the indirect methods applied in our study, we found that $\hat{M}_j$ was equal to 0.93 and that M_{cw} decreased from 2.76 at age 1 to 0.64 at age 6.

Population Size and Biomass

Estimated population sizes ($\hat{N}_i$) and biomass ($\hat{B}_i$) of Grass Carp varied widely dependent upon the method used to estimate mortality. In all years, population sizes estimated based on $\hat{M}_p$ were intermediate to and significantly different from those estimated based on $\hat{M}_j$ and M_{cw} (Figure 2). Biomass predicted based on $\hat{M}_p$ was significantly different from biomass estimated with $\hat{M}_j$ only for 2010 (Figure 3). Population sizes and biomasses estimated using $\hat{M}_j$ and M_{cw} also differed significantly in all years. Annual population sizes and biomass predicted with M_{cw} were consistently smaller than those predicted by using $\hat{M}_p$ or $\hat{M}_j$. For years of greatest disparity between estimates, population size and biomass derived from $\hat{M}_j$ were more than double those derived from M_{cw}.

TABLE 4.   Age-specific mortality rates (M_{cw}; derived by the method of Chen and Watanabe 1989) and associated 95% confidence limits (CLs) for Grass Carp in Lake Gaston.

Age	M_{cw}	Lower 95% CL	Upper 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

To assess the precision of indirect methods in comparison with direct estimation of mortality, we estimated annual biomass of Grass Carp in Lake Gaston by using five mortality rates (Kirk and Socha 2003) that were based on catch-curve analyses (Figure 4). Biomass estimated from four of the five mortality rates fell within the 95% CI for biomass estimated with M_{cw} in the present study; biomass derived from the fifth mortality rate fell within the 95% CIs for biomass values that we estimated by using $\hat{M}_j$ and $\hat{M}_p$.

We did not detect a significant relationship between Grass Carp population size in year i and hydrilla coverage in any of the time lag scenarios (i.e., $i, i + 1, \ldots, i + 5$). A significant inverse relationship existed between Grass Carp biomass at time i and hydrilla coverage in all time lag scenarios (including the zero-lag scenario) using each of the three indirect mortality estimates. The best model of hydrilla coverage in Lake Gaston was consistently achieved with a 4-year time lag between Grass Carp biomass and hydrilla coverage, regardless of the mortality estimate used (Table 5).

Grass Carp greater than age 10 accounted for 1–20% of the annual total population size, and they contributed 22% to nearly 50% of the total annual biomass from 2005 to 2010 depending on the mortality estimate used (Figure 5). The oldest age-classes of Grass Carp also appeared to have a significant effect on hydrilla coverage in Lake Gaston relative to other age-classes. The best model of the effects of Grass Carp age on the efficacy of weed control included Grass Carp of all ages up to age 16, regardless of the method used to estimate mortality (Table 6). When $\hat{M}_p$ or $\hat{M}_j$ was used to estimate biomass, the model that included ages 13–16 was over 200 times more plausible than the next-best model, which included only ages 1–8. When M_{cw} was used to estimate biomass, the model including ages 13–16 was 45 times more plausible than the model that included only ages 1–8. Based on AIC$_c$ difference (Δ_i) values, models that did not include the oldest age-group of fish had virtually no support in the data.

DISCUSSION

The collection of Grass Carp in Lake Gaston by bowfishers provided an effective means of sampling for age and growth analyses of the population, as has been previously documented (Morrow et al. 1997). However, because we lacked information on sampling effort and because there was no standardized regime for sampling Grass Carp in the lake, the Grass Carp catch
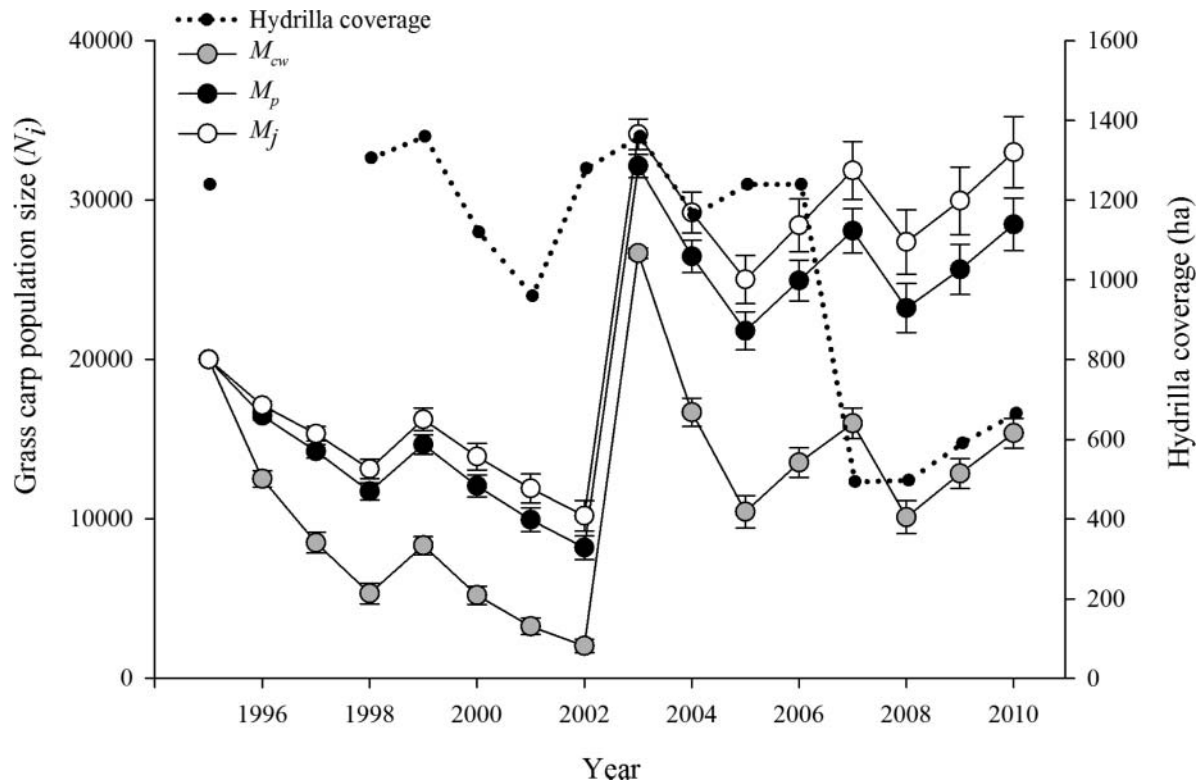
FIGURE 2.   Estimated Grass Carp population size ($\hat{N}_i$; ±95% confidence interval) in Lake Gaston during 1995–2010, presented in relation to hydrilla coverage. Population size was predicted based on (1) mean mortality (across all ages) derived by the method of Pauly (1980; $\hat{M}_p$), (2) mean mortality derived by the method of Jensen (1996; $\hat{M}_j$), or (3) age-specific mortality derived by the method of Chen and Watanabe (1989; M_{cw}).

data did not meet some of the underlying assumptions for use of direct mortality estimation methods (such as catch curves), which have been widely applied in fisheries monitoring for the last 50 years (Thorson and Prager 2011). The mortality rates reported by Kirk and Socha (2003) for the years 1998 ($M = 0.33$), 1999 (0.39), 2000 (0.35), and 2002 (0.38) produced biomass estimates for the Lake Gaston Grass Carp population that fell within the 95% CI of biomass predicted by using M_{cw} in our study. The low mortality rate of 0.22 (for 2001) reported by Kirk and Socha (2003) resulted in a predicted biomass that was within the 95% CI of biomass estimated with $\hat{M}_p$ and $\hat{M}_j$ in the present study. These results suggest that (1) the indirect methods we used to estimate mortality have precision comparable to that of direct estimation based on catch curves for other systems and (2) age-specific mortality may present more comparable estimates over the life span of Grass Carp. Although the reliability of the indirect methods we used cannot be measured against that of the estimates derived by Kirk and Socha (2003), the agreement between results of the two studies suggests that the precision achieved in the present study should be satisfactory for use in management.

The expected longevity of the population should be considered when using indirect methods of estimating mortality based on growth of triploid Grass Carp. In this study, we were able to obtain a large number of individuals of various ages for use in estimating VBGM parameters for the Lake Gaston population, resulting in well-informed parameter estimates based on data that were representative of fish approaching the maximum age in their native system (Gorbach 1961). In contrast, when we used VBGM parameters from the Santee–Cooper Reservoir population (Morrow et al. 1997) to estimate mortality with the indirect methods applied in our study, we found that estimated mortality was not within the range of estimates that were derived by using catch-curve analyses in the same system, even within the same years (Morrow et al. 1997; Kirk and Socha 2003). These results suggest that the use of VBGM parameters from populations that are short lived (or are expected to be short lived) is not an appropriate approach to mortality estimation, despite large sample sizes such as those obtained from the Santee–Cooper Reservoir population (Morrow et al. 1997; Kirk et al. 2000; Kirk and Socha 2003). Because our estimates are based on a long-lived population of Grass Carp that were stocked incrementally, they should be useful for projecting Grass Carp population sizes in other southeastern U.S. systems, especially where the goal is the intermediate control of weeds rather than eradication and where Grass Carp are stocked incrementally in sufficient numbers to persist for more than 10 years (the age accommodated by other stocking models; e.g., Stewart and Boyd 1999).
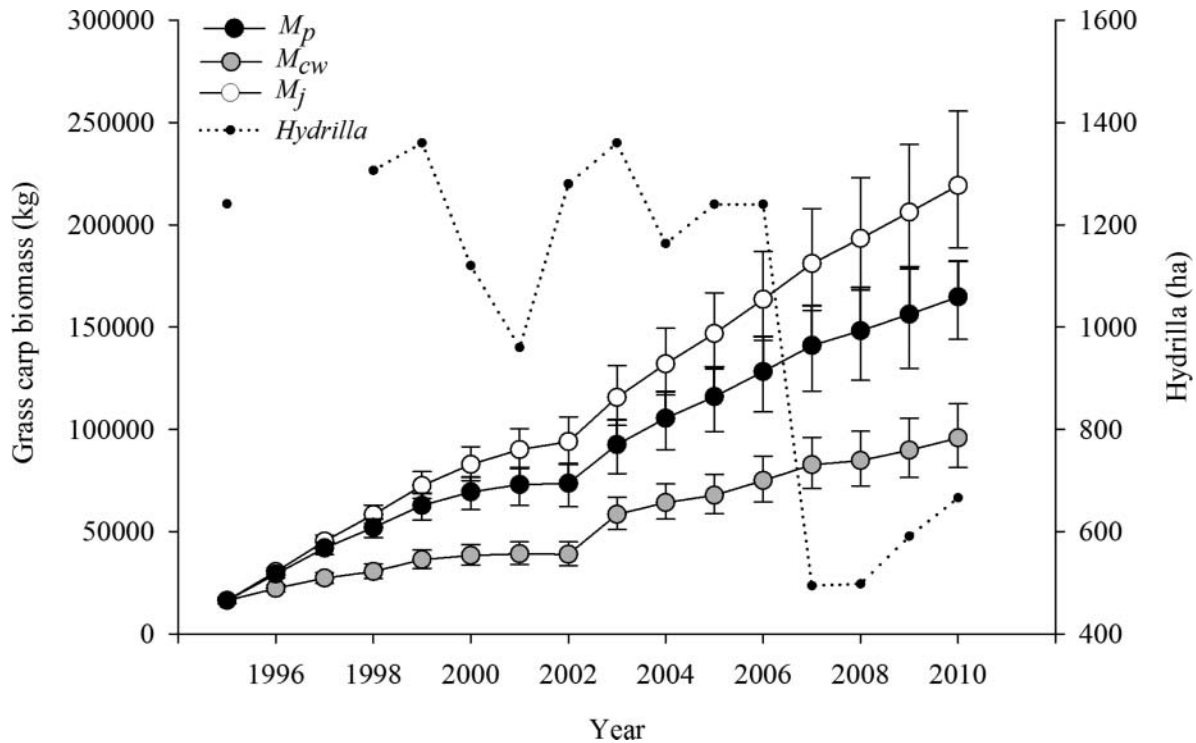
FIGURE 3. Annual hydrilla coverage in Lake Gaston during 1995–2010, presented in comparison with estimates of Grass Carp standing biomass that were derived from mortality estimated by the method of (a) Jensen (1996; $\hat{M}_j$), (b) Pauly (1980; $\hat{M}_p$), or (c) Chen and Watanabe (1989; M_{cw}). Biomass was estimated by using the mean and 95% confidence limits (CLs) for mortality at each age, and the 95% confidence interval around each biomass estimate is based on the upper and lower 95% CLs for weight at each age.

The mortality estimates and resulting biomass estimates in our study represent two somewhat divergent models of Grass Carp population dynamics in Lake Gaston. The constant instantaneous mortality estimates ($\hat{M}_p$ and $\hat{M}_j$) we obtained generally represented lower overall mortality in the Grass Carp
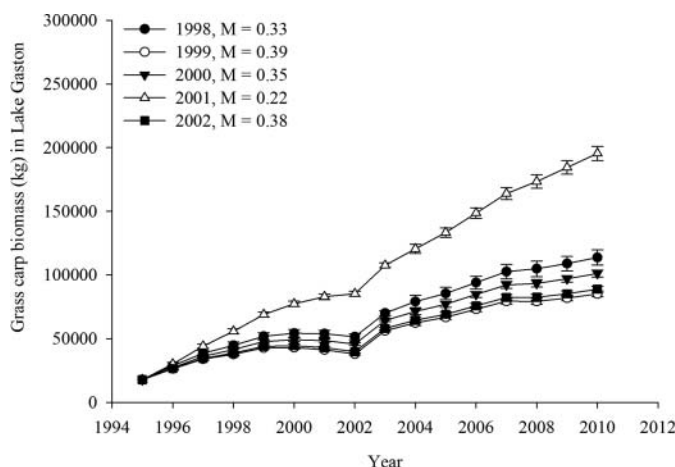

FIGURE 4. Grass Carp biomass in Lake Gaston, as projected by using five mortality estimates (1998–2002) developed for Grass Carp populations in the Santee–Cooper Reservoir system, South Carolina, via catch-curve analysis by Kirk and Socha (2003).

population and therefore resulted in biomass estimates that were higher than those derived from age-specific mortality estimates (M_{cw}). As a result of the differences in biomass estimated from these methods, we suggest that constant and age-specific mortality estimates represent two potential approaches to assessing Grass Carp in Lake Gaston, depending on how stocking rates are determined in the future. Application of age-specific mortality estimates to the Lake Gaston Grass Carp population results in a lower estimated number of fish per vegetated hectare and a smaller estimated biomass than does the use of constant mortality rates. Because the biomass estimated from age-specific mortality rates is lower, the absolute difference between current biomass and some target level of biomass would be smaller— and thus the estimated addition of biomass required for stocking would be lower—when age-specific mortality rates are used instead of a constant rate to estimate biomass. When the risk of overshooting the target hydrilla coverage is considered, the use of age-specific mortality in stocking models that are based on biomass therefore represents a more conservative approach to Grass Carp stock assessment than does the use of a constant mortality rate. Relative to the use of a constant mortality rate, the use of age-specific mortality in stock assessment and stocking models is less likely to result in overshooting the target coverage of hydrilla but is more likely to result in failure to achieve adequate control of hydrilla. Our results demonstrate that the approach to

TABLE 5.   Model selection statistics for linear regressions characterizing the relationship between Grass Carp biomass in year i and hydrilla coverage in Lake Gaston based on various time lag scenarios (i.e., coverage in years i, i + 1, ..., i + 5). Biomass was estimated from (1) constant mortality (across all ages) derived by the method of Pauly (1980; $\hat{M}_p$), (2) constant mortality derived by the method of Jensen (1996; $\hat{M}_j$), or (3) age-specific mortality derived by the method of Chen and Watanabe (1989; M_{cw}). Model selection statistics include the number of parameters estimated (k), Akaike's information criterion corrected for small sample sizes (AIC_c), the difference between the AIC_c value for the given model i and the best model (Δ_i), and Akaike weight (w_i), which describes the relative probability that the given model is the best among the models considered. Models were ranked separately for each mortality estimate.

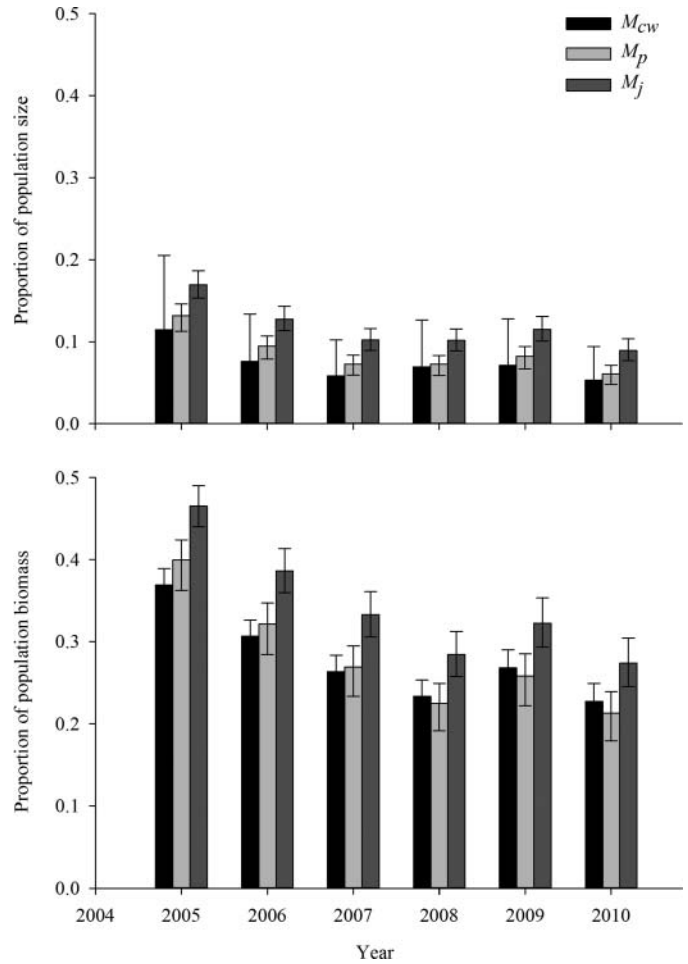| Mortality estimate	Lag time (years)	k	AIC_c	Δ_i	w_i
M_{cw}	0	2	186.8	19.1	0.00
	1	2	187.8	20.1	0.00
	2	2	185.3	17.6	0.00
	3	2	181.2	13.5	0.00
	4	2	167.7	0.0	1.00
	5	2	180.8	13.1	0.00
M_p	0	2	193.2	13.8	0.00
	1	2	193.2	13.8	0.00
	2	2	191.6	12.2	0.00
	3	2	188.1	8.7	0.01
	4	2	179.4	0.0	0.96
	5	2	186.8	7.4	0.02
M_j	0	2	198.7	19.3	0.00
	1	2	198.7	19.3	0.00
	2	2	197.1	17.7	0.00
	3	2	193.7	14.3	0.02
	4	2	186.0	6.6	0.92
	5	2	191.7	12.3	0.05

FIGURE 5.   Proportion of the Grass Carp population size accounted for by individuals older than age 10 (upper panel) and the proportion of Grass Carp population biomass contributed by individuals older than age 10 (lower panel) in Lake Gaston. Population size and biomass were estimated by using mortality derived from the methods of Pauly (1980; $\hat{M}_p$) and Jensen (1996; $\hat{M}_j$) across all ages or by using age-specific mortality derived from the method of Chen and Watanabe (1989; M_{cw}).

Grass Carp stock assessment (i.e., the mortality estimator used) is dependent upon the specific weed control objectives.

Our results indicate that Grass Carp biomass is a more appropriate index of fish density than Grass Carp abundance. We failed to detect a relationship between Grass Carp abundance and annual hydrilla coverage in Lake Gaston under any of the time lag scenarios. We did, however, observe strong negative relationships between Grass Carp biomass and hydrilla coverage under all of the time lag scenarios. The biomass–hydrilla coverage relationship was strongest when we considered a 4-year lag between Grass Carp stocking and observed effects on hydrilla coverage. Because the 4-year lag scenario was the best model regardless of whether biomass was estimated from age-specific mortality or from a single mortality rate, we suspect that the lag is not a result of age-specific changes in mortality. As all of the lag scenarios provided a good fit to the data, we speculate that the importance of a 4-year lag is not based simply on the Grass Carp population attaining a threshold biomass at which hydrilla reduction is achieved. Bioenergetics studies of Grass Carp have demonstrated that the feed assimilation rate is inversely related

to mass, whereas the standard metabolic rate and energy per gram of wet weight are positively related to mass (Wiley and Wike 1986). These factors cause an increase in the energy required per unit of mass gained by Grass Carp as they grow larger; greater energetic requirements necessitate increased hydrilla consumption by the fish in Lake Gaston. Growth of Grass Carp has been observed to decrease after age 4 in native systems (Gorbach 1961). However, growth (in mass) of Grass Carp in Lake Gaston remained approximately linear with age after age 4, thus amplifying the increase in energy needed for growth after that age. Therefore, the 4-year lag between Grass Carp stocking and observable effects on hydrilla coverage likely reflects an increase in hydrilla consumption due to the greater energetic demands of Grass Carp for maintenance of linear growth in mass after they reach age 4.

TABLE 6. Model selection statistics for multiple linear regression models used to determine the relative effects of Grass Carp biomass at different ages on the hydrilla coverage in Lake Gaston. Biomass was estimated from (1) constant mortality (across all ages) derived by the method of Pauly (1980; $\hat{M}_p$), (2) constant mortality derived by the method of Jensen (1996; $\hat{M}_j$), or (3) age-specific mortality derived by the method of Chen and Watanabe (1989; M_{cw}). Models are defined in Table 1; model selection statistics are defined in Table 5. Models were ranked separately for each mortality estimate.

Mortality estimate	Model	k	R^2	AIC_c	Δ_i	w_i
M_{cw}	Hydrilla (B_4)	2	0.00	209.4	18.9	0.000
	Hydrilla ($B_4 + B_8$)	3	0.67	198.1	7.6	0.022
	Hydrilla ($B_4 + B_8 + B_{12}$)	4	0.67	202.9	12.4	0.002
	Hydrilla ($B_4 + B_8 + B_{12} + B_{16}$)	5	0.92	190.5	0.0	0.976
M_p	Hydrilla (B_4)	2	0.01	209.4	19.2	0.000
	Hydrilla ($B_4 + B_8$)	3	0.63	199.7	10.7	0.005
	Hydrilla ($B_4 + B_8 + B_{12}$)	4	0.63	204.7	15.7	0.000
	Hydrilla ($B_4 + B_8 + B_{12} + B_{16}$)	5	0.92	189.9	0.0	0.995
M_j	Hydrilla (B_4)	2	0.01	209.4	19.2	0.000
	Hydrilla ($B_4 + B_8$)	3	0.59	200.9	10.7	0.005
	Hydrilla ($B_4 + B_8 + B_{12}$)	4	0.59	205.9	15.7	0.000
	Hydrilla ($B_4 + B_8 + B_{12} + B_{16}$)	5	0.92	190.2	0.0	0.995

The lag between Grass Carp stocking and observed effects on hydrilla coverage is likely different than the lags present in other systems, such as Lake Austin and Lake Conroe in Texas (Chilton and Magnelia 2008; Chilton et al. 2008) and the Santee–Cooper Reservoir system (Kirk et al. 2000; Kirk and Socha 2003), because stocking densities are much lower in Lake Gaston than in these other systems. For example, Lake Conroe (8,347 ha; Chilton et al. 2008) is similar in size to Lake Gaston (8,423 ha) but received 371,766 diploid and triploid Grass Carp from 1982 to 2007 (Chilton et al. 2008), whereas only 92,959 triploid Grass Carp were stocked in Lake Gaston from 1995 to 2011. The Santee–Cooper Reservoir system (70,000 ha) is considerably larger than Lake Gaston, and it received the single largest Grass Carp stocking (786,500 fish) in history (Kirk et al. 2000).

We recognize that the Grass Carp biomass–hydrilla coverage relationship reported here is singular and correlative in nature and that it cannot be used to infer a cause-and-effect relation (i.e., because this is an observational study). However, given the dependency of Grass Carp on hydrilla as their primary energy source, the strength of the observed relationship ($R^2 > 0.90$), and the expansive time series used, we believe that this relationship is a useful means of monitoring the progress of weed control efforts in Lake Gaston. In fact, the regression relationship based on Grass Carp standing biomass was useful for predicting the Lake Gaston hydrilla coverage within 40 ha of the coverage that was estimated with sonar surveys conducted in 2010 and 2011 (D. S. Stich, unpublished data). The unexplained portion of variation in the biomass–hydrilla coverage relationship is likely due to environmental variation during the 16 years represented. We also recognize the potentially confounding effects of the low-level herbicide application that occurred in conjunction with Grass Carp stocking in Lake Gaston. Because the relationship between Grass Carp biomass and hydrilla coverage is subject to confounding factors like herbicide application, we cannot speculate whether the relationship observed in our study is necessarily transferable to other water bodies.

Although Grass Carp in Lake Gaston appear to have reduced the amount of hydrilla to below peak coverage, the management objective of 120 ha by 2012 was not met. The problem of reaching a target level of hydrilla without overshooting it suggests that there are specific situations in which an aggressive approach to weed control at Lake Gaston may give way to a more conservative model and vice versa. It is difficult to predict the time period (if any) over which the target level of hydrilla coverage will be reached at the current stocking rate for Grass Carp in Lake Gaston; it is possible that the stocking rate will have to be increased in order to reach the target level of coverage.

Stocking models that are more refined than the monitoring tools we present here are available; such models are useful for estimating the numbers of Grass Carp needed to control a given coverage of hydrilla over time (e.g., Stewart and Boyd 1999), but these models apply only to the first 10 years after stocking. Based on the bioenergetics of Grass Carp (Wiley and Wike 1986) and the linear patterns of weight gain observed in Lake Gaston and other systems (e.g., Morrow et al. 1997), it is likely that Grass Carp older than age 10 also make important contributions to weed control. In Lake Gaston, fish exceeding age 10 made substantial contributions to the total biomass—but not the number—of Grass Carp in the system. The first year in which Grass Carp older than age 10 were present in Lake Gaston was 2005. After 2005, Grass Carp that were older than age 10 accounted for more than 22% of total estimated standing biomass in each year, regardless of the mortality estimate used; in some years and under some mortality scenarios, fish older than age 10 accounted for nearly 50% of the total estimated population biomass. In most years, the older fish contributed less than 10% and as little as 1% (depending on the model used)

to the total number of Grass Carp in the system. Since weight gain of Grass Carp in Lake Gaston is approximately linear with age, there is reason to believe that fish up to at least age 16 continue to provide some control of aquatic weeds and should therefore be considered in stocking models. Other research has speculated that large Grass Carp (up to 10 kg) may be just as effective for weed control as small fish (Osborne and Riddle 1999). Our regression models of hydrilla coverage response to various age-groups confirm this for fish up to at least age 16; the strongest model of hydrilla coverage was based on Grass Carp biomass estimates that included fish up to 16 years of age. The contribution of Grass Carp to weed control through age 16 in Lake Gaston highlights the need for all ages to be included in stocking models and bioenergetics models, especially as IPM becomes increasingly prevalent and as management of long-lived Grass Carp becomes more commonplace.

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