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# Life, Death, and Resurrection: Accounting for State Uncertainty in Survival Estimation from Tagged Grass Carp

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ARTICLE

# Life, Death, and Resurrection: Accounting for State Uncertainty in Survival Estimation from Tagged Grass Carp

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***Abstract***
**Information about Grass Carp *Ctenopharyngodon idella* survival would be useful for improving the management of fish used for aquatic weed control. Reliable methods for estimating annual poststocking survival of Grass Carp from radiotelemetry data do not exist because the fish remain sedentary for prolonged periods between movements, giving the false impression of death, only to be observed alive (i.e., "resurrected") at a later date. We constructed a state-space, multistate mark–recapture survival model accounting for uncertainty in the live/dead states of tagged Grass Carp in a large (8,500 ha) reservoir, and we estimated monthly and annual survival. Model results were compared with life history-based methods for estimating survival, and survival estimates that were corrected for state misclassification were compared with uncorrected estimates. Corrected estimates of annual survival (mean = 0.23; 95% credible interval [CRI] = 0.15–0.41) contained less bias than uncorrected estimates (0.12; 95% CRI = 0.08–0.18). However, both corrected and uncorrected estimates were substantially lower than the survival expected based on life history theory (mean = 0.69; 95% confidence interval = 0.52–0.78), suggesting that mark–recapture survival estimates for Grass Carp might be negatively biased due to tag shedding, tag-related mortality, or both. Our model effectively reduced bias in monthly and annual survival estimates due to state misclassification, illustrating the potential for application of existing mark–recapture frameworks to estimate Grass Carp survival with telemetry data, despite the behavioral idiosyncrasies of the species. Furthermore, these methods may have application for studies of other animals that undergo periodic quiescence between movements, such as salmonids, ictalurids, and reef fishes. To account for bias resulting from tag loss, future mark–recapture studies of Grass Carp could incorporate tag shedding rates within the framework developed here.**

Stocking rates of triploid Grass Carp *Ctenopharyngodon idella* used for weed control have varied greatly based on factors such as weed coverage, temperature, fish size, and variability in estimates of survival (Allen and Wattendorf 1987). Information about the survival of triploid Grass Carp in the first year after release could provide managers with valuable insight into factors influencing the cost and effectiveness of stocking strategies. Studies that have attempted to quantify Grass Carp poststocking survival to inform weed management have resulted in survival estimates that are widely variable (from 0.05 to 0.97) due to variability in stocking strategies, climates, and estimation error (Clapp et al. 1994).

Although several methods have been used to estimate Grass Carp survival retrospectively using annual time-series data (e.g., Morrow et al. 1997; Kirk et al. 2000; Stich et al. 2013), none of those methods can provide estimates of poststocking survival based on only a single year of information. In most systems, Grass Carp survival estimates are not verified through multiple approaches, although verification could potentially benefit management due to (1) the uncertainty surrounding all

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types of survival estimation (Vetter 1988) and (2) the precarious dependence of triploid Grass Carp population dynamics models on stocking rates and survival estimates as the sole determinants of predicted population size. By comparing poststocking survival estimates that are derived using multiple approaches, managers would have more information at their disposal and could improve decision making about stocking densities for this species. Consistency between estimates might also improve confidence in the quality of information used for decision making.

One useful method for estimating the poststocking survival of fish is the recapture of marked individuals at some time or series of occasions after stocking (e.g., through use of Cormack–Jolly–Seber models; Jolly 1965; Seber 1965). However, due to difficulties associated with the capture of Grass Carp (Colle et al. 1978; Schramm and Jirka 1986; Bonar et al. 1993), traditional mark–recapture methods requiring the physical recapture of fish can result in biased or imprecise estimates of survival (Colle et al. 1978; Stott and Russell 1979). Capture of Grass Carp is difficult even in small systems and becomes increasingly difficult as system size increases (Bonar et al. 1993). Recent advances in the analysis of biotelemetry data have resulted in reliable methods for estimating survival from tagged animals (Pollock et al. 1989, 1995; Pine et al. 2003). These methods have been widely applied to other fish and wildlife populations (Pine et al. 2003), and they appear to be useful for estimating the survival of Grass Carp after release, even in relatively large systems.

Several studies of Grass Carp have reported a high incidence of presumed mortality (as much as 50%: Maceina et al. 1999) based on the lack of movement by fish (Bain et al. 1990; Chilton and Poarch 1997; Maceina et al. 1999; Kirk et al. 2001). In other radiotelemetry studies, some Grass Carp that were thought to be dead were later verified as alive based on their movement (Bain et al. 1990). Grass Carp undergo long periods of quiescence between periods of activity. Chilton and Poarch (1997) observed many Grass Carp that moved less than 15 m during a 24-h period despite being alive. Such behavior has precluded reliable estimation of survival for tagged Grass Carp. With the development of mortality-sensing tags, it is now theoretically possible to determine whether or not an animal is alive based on combined information from the rate of radio signal transmission and the detected movements of an animal (Kenward 2001). Mortality sensors in radio tags often rely on the movement of fish, but Grass Carp commonly remain sedentary long enough to activate the sensor without actually dying. This creates challenges for estimating the survival of tagged Grass Carp, as it can be difficult to determine whether an individual is alive or dead, even when combining information from the mortality-sensing radio tags with the current knowledge about this species' behavior. As such, researchers must be able to account for uncertainty in the assignment of live and dead states when estimating survival from sedentary, tagged fish. Recent research has used multistate (MS) models to demonstrate the effects of state uncertainty on estimation of demographic rates in wildlife populations (Nichols et al. 2007; Kendall 2009; Mackenzie et al. 2009). In the present study, we did indeed observe Grass Carp whose tags were transmitting a mortality signal (as indicated by an increased transmission rate) at one time and that were subsequently relocated more than 20 km away. Therefore, survival models that use information from the mortality sensors need to allow for state misclassification; otherwise, estimates might be negatively biased.

The objectives of this study were to (1) determine how the sedentary behavior of Grass Carp influences our ability to accurately assess whether an individual is alive or dead; and (2) quantify how misclassification might influence estimation of poststocking survival for tagged Grass Carp. To achieve these objectives, we created a hierarchical (state-space) MS mark–recapture model to estimate poststocking survival of tagged Grass Carp. To quantify effects of bias due to uncertainty in state assignment resulting from the Grass Carp's sedentary behavior, we compared corrected survival estimates to uncorrected estimates. We then compared model predictions to estimates from the same system that were based on established methods for estimating fish survival from life history theory.

## METHODS

*Study site*.—Lake Gaston, located on the border of North Carolina and Virginia, is a large (8,500 ha) impoundment of the Roanoke River. Hydrilla *Hydrilla verticillata* is a noxious weed that was discovered in Lake Gaston in 1992 (Ryan et al. 1995). Aerial coverage of hydrilla peaked in 2003 at 1,364 ha despite weed management efforts that began in the early 1990s. Stocking of Grass Carp as part of the weed management plan began in 1995 (Richardson 2008) and continues to the present, in combination with annual herbicide applications. The goal of the weed management plan for Lake Gaston is not the complete eradication of hydrilla. Instead, the management goal for hydrilla control is "to develop and maintain a healthy lake ecosystem based on a diverse plant community dominated by native species" (Lake Gaston Stakeholders Board 2005). To achieve this goal, one of the stated objectives of management is to reduce hydrilla coverage to 120 ha.

From 1995 through 2013, slightly fewer than 100,000 triploid Grass Carp were stocked incrementally into Lake Gaston as part of the integrated approach to hydrilla management. Lake managers are averse to the overstocking of Grass Carp because complete eradication of all submersed vegetation would be undesirable to some stakeholders and would not achieve the primary goal of weed control in the system (Richardson 2008). However, recent estimates of survival do not allow for the fine tuning of annual stocking rates to better address plant control objectives; this is because of the time required to collect the necessary data and because the selected methods cannot be used to explain within-year variability in survival. Surface coverage of hydrilla in Lake Gaston during 2013 (about 230 ha; ReMetrix 2014) was approaching the 120-ha target level. As such, reliable information about the survival of Grass Carp in the first year after stocking is needed to guide future stocking decisions as part of an adaptive approach to weed management (Lake Gaston Stakeholders Board 2005); however, a working framework for quantifying the effects of management actions is needed first. Mark–recapture studies offer a possible framework for studying individual-based and annual changes in Grass Carp survival.

*Radio-tagging and radiotelemetry*.—We tagged Grass Carp by using two different procedures (internal implant or external attachment). In 2007 ($n$ = 29 fish) and 2008 ($n$ = 32 fish), Grass Carp were subject to surgical implantation of mortality-sensing radio tags with trailing-whip antennae (Model F1820; Advanced Telemetry Systems, Isanti, Minnesota). The tags were implanted by using a midventral-implant procedure previously documented by Schramm and Black (1984) that was adapted to accommodate smaller tags than were used in that study (i.e., we used smaller incisions and fewer sutures). Tags had an estimated battery life of 2–6 years, and tag mass was dependent upon expected battery life (8 or 25 g in air, respectively). As recommended by Winter (1996), radio tag weight never exceeded 2% of fish body weight. In 2009, we again used surgical implantation for 15 fish, but we also fitted 25 fish with external radio tags (see Thorstad et al. 2013). The timing and locations of tagged Grass Carp releases coincided with the stocking of untagged Grass Carp during each year of this study. After stocking, tagged fish were tracked at least monthly for a minimum of 1 year; the exception was February 2010, when weather prevented travel to the lake in the period during which tags were actively transmitting. An aerial survey conducted by plane in 2008 indicated that there was no emigration of tagged Grass Carp from the reservoir.

*Multistate mark–recapture model description*.—We constructed monthly capture histories for each tagged Grass Carp by recording whether the fish was found alive, was found with a tag transmitting a mortality signal, or was unobserved in each month. Grass Carp were assigned to a "live" state when they were found with a tag transmitting at a normal rate; they were assigned to a "dead" state when found with a tag transmitting a mortality signal. Because of missing location data (i.e., imperfect detection), we could not use a classic known-fate model (Pollock et al. 1989) for analysis; therefore, we adapted methods developed by Devineau et al. (2010) to estimate Grass Carp survival within the MS mark–recapture framework using hierarchical (state-space) models (Kéry and Schaub 2012). Multistate models allow for the separate estimation of survival ($\phi$) and transitions between live and dead states ($\psi$) while accounting for imperfect detection ($p$) of tagged animals in each state. Due to the general structure of MS models, survival rates can be estimated either from survival parameters or as transition probabilities between states when live and dead states are used. Because the detection of radio-tagged fish was imperfect, we fixed survival probabilities in the MS models to 1.0 in both the live and dead states, and we estimated survival as 1.0 minus the probability of transitioning from the live state to the dead state (Devineau et al. 2010). Since it is impossible for dead fish to re-enter the live state, the probability of transitioning from the dead state to the live state was fixed at zero (Devineau et al. 2010, 2014). The probability of detection was estimated separately for each state.

TABLE 1. State process matrix showing the probability of Grass Carp being in state $h'$ at time $t+1$ given survival ($\phi$) in state $h$ at time $t$ and the probability ($\psi$) of moving between states each month (adapted from Kéry and Schaub 2012). When classified in the absorbing state Grass Carp are truly dead.

| | State at time $t+1$ | | |
|---|---|---|---|
| True state at time $t$ | Live | Dead | Absorbing state |
| Live (1) | $(1-\psi_t^{1,2})$ | $\psi_t^{1,2}$ | 0 |
| Dead (2) | 0 | 1 | 0 |
| Absorbing state (3) | 0 | 0 | 1 |

One important assumption of MS mark–recapture models is that the states of individuals are observed without error. Because this was known not to be the case for Grass Carp in our study, we needed to account for state misclassification in MS models; this can be accomplished by including the probability that live fish are correctly classified as being alive ($\delta$) because state misclassification is one-directional (Kendall 2009). Thus, the MS model used for this study was a state-space adaptation of that used by Devineau et al. (2010) and discussed by Devineau et al. (2014), but it was also corrected for one-way state misclassification as outlined by Kendall (2009).

The MS models included an observation process model for Grass Carp detection probability that was conditional on the true state of the individuals, which was modeled by a state process model (Kéry and Schaub 2012). The likelihoods for each of the component models (state process and observation process models) were multinomial but with only a single trial for each individual; the probability of being in a state and the probability of being detected in that state were both modeled as categorical distributions.

The state process for the MS model developed in this study included three possible states in which a fish could exist and move between each month: (1) live (tag transmitting a "live" signal), (2) dead (tag transmitting a mortality signal), or (3) unobserved. In the state process matrix of the MS survival models (Table 1), the probability of occupying a given state $h$ at a given time ($t+1$) was based on the state of an individual $i$ at the previous time ($t$); the probability of survival in state $h$ during time $t$ ($\phi_t^h$); and the probability of moving from state $h$ to another state ($h'$) after time $t$ given survival during time $t$ ($\psi_t^{h,h'}$). Thus, the state process model was conditioned on the state at the first encounter (i.e., live for all fish). Due to limited sample sizes and the large number of parameters that otherwise would have to be estimated, all parameters were held constant across all time intervals (i.e., in each month) of the study. Therefore, a single $\hat{\psi}_t^{1,2}$ was estimated, representing an uncorrected (for misclassification) monthly estimate based on the constraints imposed (above), and it was used to calculate uncorrected monthly survival as $1 - \hat{\psi}_t^{1,2}$ and uncorrected annual survival ($\hat{S}_u$) as $\left(1-\hat{\psi}_t^{1,2}\right)^{12}$. These values were compared with the corrected estimates of monthly and annual survival described below. The likelihood for the state process model was defined (see Kéry and Schaub 2012) as

$$z_i fs_i = fs_i \tag{1}$$

and

$$z_{i,t+1} \mid z_{i,t} \sim \text{categorical}\left(\Omega_{z_{i,t},1\ldots S,i,t}\right), \tag{2}$$

where $z_{i,t}$ is the true state of each individual $i$ at time $t$; and $f$ is the state ($s$) of each fish at the first encounter. The probability of an individual's true state is a categorical distribution described by the four-dimensional matrix $\Omega$, in which the first dimension is the observed state $z$ at time $t$, the second dimension is the vector of true states ($1,\ldots, S$) at time $t + 1$, the third dimension is the individual fish $i$, and the fourth dimension represents time $t$ (see Kéry and Schaub 2012).

The observation process for the MS survival model developed in this study was conditional on the state process and included three possible states used in constructing the encounter histories: (1) live; (2) dead (tag transmitting a mortality signal); and (3) unobserved (Table 2). Detection probability ($p_t^h$) was estimated as the probability of a fish being observed in state $h$ during time $t$ given that the fish was in state $h$ during time $t$ (Table 2). We assumed that detection of fish that truly occupied state 2 (dead) had no error associated with it (i.e., a "live" signal could not be transmitted from dead fish). Therefore, the probability of detecting a dead fish in the live state ($p_t^{1|2}$) was fixed at zero. Prior distributions on all remaining detection probabilities ($p_t^{1|1}$, $p_t^{2|1}$, and $p_t^{2|2}$) were assigned as random uniform distributions between zero and 1.0. The probability that a live fish was correctly classified as being in the live state ($\delta$) was incorporated directly into the observation process matrix (Table 2) and was assigned a uniform prior between zero and 1.0. The likelihood for the observation process conditional on the state was defined (see Kéry and Schaub 2012) as

$$y_{i,t} \mid z_{i,t} \sim \text{categorical}(\Theta_{Z_{i,t},1\ldots O,i,t}), \tag{4}$$

where $y$ is the observed state of individual $i$ at time $t$ given the actual state $z$ of that individual at time $t$; and $y$ is defined to have a categorical distribution described by the four-dimensional matrix $\Theta$. The first element of $\Theta$ is the vector of true states, the second is the vector of observed states ($O$), the third is the individual fish $i$, and the fourth is time $t$ (Kéry and Schaub 2012).

For the final dead detection of a given fish, the probability that the true state of the fish was "dead" was confounded with the probability that the fish was correctly assigned to that state because there were no observations of that fish thereafter. Therefore, the corrected estimate of monthly survival needed to account for fish that were last observed in the dead state but were not dead. To do this, we adjusted our estimate of monthly survival ($1 - \psi_t^{1,2}$) by the probability that fish were detected in either the live state or the dead state and by the probability that the fish was correctly classified:

$$\begin{aligned}\hat{S}_t \;=\; 1 - \;\hat{\psi}_t^{1,2}[\hat{p}_t^{1|1}\hat{\delta}_t - \;\hat{p}_t^{2|1}(1 \;-\; \delta_t)]\\ - [(1 - \;\hat{p}_t^{2|1}\hat{\delta}_t) - (1 - \hat{p}_t^{2|1})],\end{aligned} \tag{5}$$

and the corrected annual survival rate ($\hat{S}_c$) was calculated as $\left(\hat{S}_t\right)^{12}$.

To estimate parameters of the MS model, we used Markov chain–Monte Carlo methods implemented in JAGS by using the R2Jags package in R version 3.1.1 (R Development Core Team 2014). We ran three Markov chains for each parameter and chose random starting values for each chain from the prior distribution of each parameter. We used a burn-in of 3,000 samples and then simulated another 30,000 samples from the posterior distribution of each parameter, keeping only every third sample to reduce autocorrelation among samples and to increase the number of independent samples (effective sample size; Kruschke 2011). This resulted in a total of 1,000 burn-in samples in each chain and 10,000 samples from the posterior distribution of each chain for each estimated parameter, yielding a total of 30,000 samples from which to construct the posterior distribution of each parameter. To diagnose the convergence of Markov chains for each parameter, we inspected trace plots of the chains to qualitatively assess the degree of mixing (agreement) between chains, and we also examined the value of the Gelman–Rubin convergence diagnostic ($\hat{r} \approx 1.00$ at convergence). The number of independent samples drawn from the posterior distribution of each parameter was used to assess the degree of

TABLE 2. Probability of observation for each state at each time $t$ given the true state of an individual Grass Carp (adapted from Kendall et al. 2012). Detection probability in each state during each time is given as $p$; $\delta$ is the probability that Grass Carp were correctly classified as being in the live state.

| | Observed state at time $t$ | | |
|---|---|---|---|
| True state at time $t$ | Live | Dead | Not detected |
| Live (1) | $p_t^{1|1}\delta$ | $p_t^{2|1}(1-\delta)$ | $1-p_t^{1|1}$ |
| Dead (2) | 0 | $p_t^{2|2}$ | $1-p_t^{2|2}$ |
| Not detected (3) | 0 | 0 | 1 |

autocorrelation between random samples and to ensure that the posterior distribution was representatively sampled (Kruschke 2011).

*Simulations for model validation*.—Because we were unable to find examples of the implementation of MS models that used live and dead states and that also included state misclassification, we felt that it was necessary to validate our model's predictions independent from other methods of mortality estimation (see below). Before applying the model to radio-tagged Grass Carp in Lake Gaston, we used a simulation-based approach to model validation, which allowed us to ensure that the model-derived estimates were not biased. We simulated capture histories for 100 virtual fish (to reflect the sample size used in Lake Gaston), assuming that survival probabilities ($\phi$) were equal and fixed at 1.0 for both the live and dead states (Figure 1). We simulated survival as 1 minus the probability of transitioning $\left(\psi_t^{1,2}\right)$ from the live state (state 1) to the dead state (state 2), and we fixed $\psi_t^{2,1}$ at zero for the simulation. Survival $\left(1-\psi_t^{1,2}\right)$ was varied from 0.50 to 0.95 to ensure that the simulation sampled a wide range of survival probabilities. We allowed for imperfect detection in the simulation by varying detection probabilities for each state independently from 0.50 to 0.95. Finally, we allowed the probability of correct classification ($\delta_t$) to vary from 0.50 to 0.95 in our simulations to create capture histories under a wide variety of misclassification rates. We ran the simulation 10,000 times to ensure adequate (i.e., representative) sampling of the parameter space for each input. For each run, random values of $\psi_t^{1,2}$, $p_t^1$, $p_t^2$, and $\delta_t$ were drawn from uniform probability distributions defined by the ranges described above. Model parameters were estimated using the same methods as described above. Bias was calculated as the mean of the posterior distribution of $\hat{S}_c$ minus the true value of $\left(1-\psi_t^{1,2}\right)$ used to simulate data (Figure 1).

*Model assumptions*.—Some telemetry studies of Grass Carp have reported high numbers of stationary tags due either to a high occurrence of tag shedding or to high fish mortality (Clapp et al. 1993; Maceina et al. 1999; Prentice et al. 2000). Tag loss has also been observed in Grass Carp that were tagged internally for controlled experiments; rupturing of the sutures was identified as the primary mechanism for tag loss in about 20% of tagged fish (Schramm and Black 1984). This is a violation of the assumptions made for mark–recapture modeling.

Survival estimates derived using telemetry-based methods could have been negatively biased in the present study if the probability of tag shedding or tagging-induced mortality was high. To assess the potential degree of bias in telemetry estimates resultant from tag shedding or tag-related mortality, estimates of annual survival for Grass Carp in Lake Gaston from radiotelemetry models were compared with life history-based survival estimates based on data from a previous study (Stich et al. 2013). Using 16 years of growth data from Grass Carp in Lake Gaston, Stich et al. (2013) estimated von Bertalanffy growth parameters (von Bertalanffy 1938), including the Brody growth coefficient ($K$), the theoretical age of fish at a length of zero ($t_0$), and the maximum observed age ($t_{max}$), and subsequently estimated average annual mortality at each

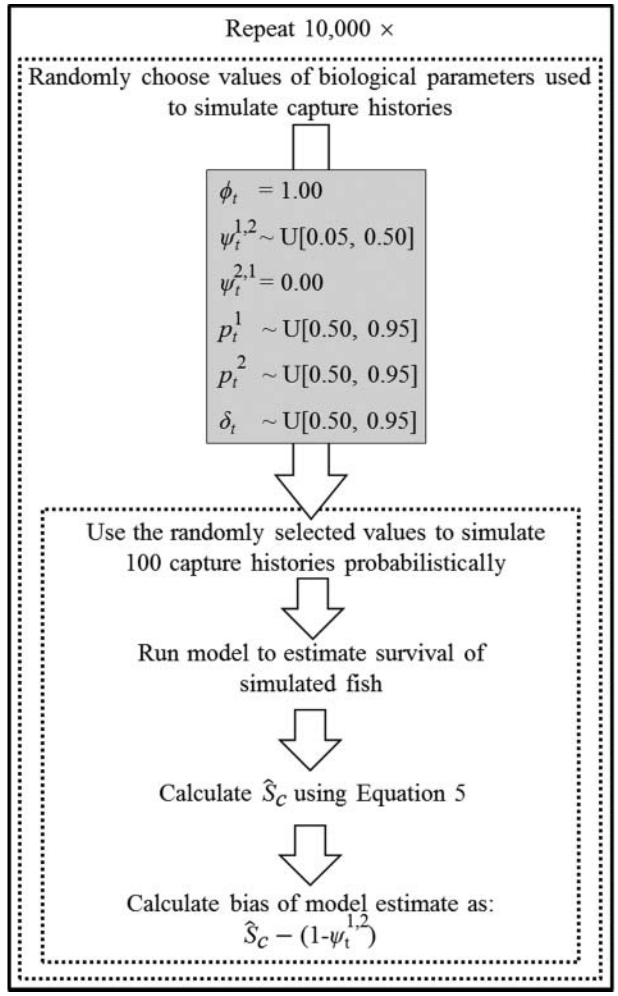


FIGURE 1. Schematic diagram of the process used to simulate capture histories for virtual Grass Carp based on a wide range of biological parameters, including probability of transitioning from the live state (state 1) to the dead state (state 2) before month $t+1$ ($\psi_t^{1,2}$), detection probabilities in each state ($p_t^1$ and $p_t^2$), and the correct classification rate ($\delta_t$) for live fish that were detected. We estimated the probability of survival as a state transition rate ($1-\psi_t^{1,2}$), so the parameter conventionally used to estimate survival probability ($\phi_t^h$) in each state $h$ was fixed at 1.0, and the probability of moving from the dead state to the live state ($\psi_t^{2,1}$) was fixed at zero. For each model run, a random value was drawn from a uniform distribution describing each of the remaining parameters (uniform distribution for each is shown in the gray box). With those values, capture histories were probabilistically simulated using the methods described by Kéry and Schaub (2012). The capture histories were then used as model input to estimate the corrected monthly survival rate ($\hat{S}_c$) with equation (5), and $\hat{S}_c$ was compared with the known value of survival used to simulate the data ($1-\psi_t^{1,2}$), allowing us to assess the degree of bias from the model over 10,000 iterations.

age $t$ based on those parameters:

$$S_{(t)} = 1 - \begin{cases} 1 - \dfrac{K}{1 - e^{-K(t - t_0)}} & \text{if } t < t_{max} \\ \dfrac{K}{a_0 + a_1(t - t_{max}) + a_2(t - t_{max})^2} & \text{if } t \geq t_{max}, \end{cases} \quad (6)$$

where $a_0$, $a_1$, and $a_2$ are constants pertaining to senescence (see Chen and Watanabe 1989). In the present study, the von Bertalanffy growth model was rearranged and maximum likelihood estimation was used to predict Grass Carp age $t$ from the length at age ($L_t$), the maximum theoretical length ($L_\infty$), and $K$ (see Mackay and Moreau 1990 for mathematical proof):

$$t = -\frac{1}{K} \times \log_e\left(1 - \frac{L_t}{L_\infty}\right) + t_0. \quad (7)$$

The exact length-at-age data described by Stich et al. (2013) for 243 Lake Gaston Grass Carp (ages 1–16) were used in this study to optimize the fit of the inverse von Bertalanffy growth function by using the nls package in R (R Development Core Team 2014). Mean total length (mm; ±95% confidence interval [CI]) of tagged Grass Carp was then used to estimate mean age (years; ±95% CI), which in turn was used to estimate mean annual survival (±95% CI) of tagged Grass Carp by using the methods of Chen and Watanabe (1989). The life history-based survival estimates were compared with the survival estimates from the telemetry model to assess potential bias due to either tagging-related mortality or tag shedding.

## RESULTS

### Simulation

The MS model developed in this study was asymptotically unbiased based on our simulations and effectively eliminated error resulting from the misclassification of live fish observed with radio tags that were transmitting mortality signals (Figure 2). The mean survival estimation error from 10,000 simulations using our MS model and a sample size of 100 fish was 0.0029 (Figure 2). The estimation error resulting from the model was normally distributed and centered on zero over a wide range of mortality rates, detection probabilities, and correct classification rates (see Figure 1). Thus, the method appeared to be unbiased, and any bias resulting from the use of our model was much less than the expected precision with which survival could be estimated from the Grass Carp telemetry model.

### Telemetry Model

Model diagnostics indicated that Markov chains converged for all estimated parameters and that autocorrelation between samples was adequately accounted for by thinning. Values of $\hat{r}$ were approximately 1.00 for all parameters, indicating model convergence (Table 3). Visual inspection of trace plots also indicated that the Markov chains converged, as they were thoroughly mixed for all estimated parameters.

TABLE 3. Mean, SD, 95% credible interval (CRI), Gelman–Rubin convergence diagnostic ($\hat{r}$), and number of independent samples ($n$) for each parameter estimated in the multistate mark–recapture model of Grass Carp survival in Lake Gaston ($\hat{\delta}_t$ = probability that individuals were correctly classified; $\hat{S}_c$ = corrected monthly survival probability; $\hat{p}_t^{1|2}$, $\hat{p}_t^{2|1}$, and $\hat{p}_t^{2|2}$ = probabilities of detection in each state [state 1 = live; state 2 = dead]; $\hat{\psi}_t^{1,2}$ = monthly probability of transitioning from the live state to the dead state).

| Parameter | Mean | SD | 95% CRI Lower | 95% CRI Upper | $\hat{r}$ | $n$ |
|---|---|---|---|---|---|---|
| $\hat{\delta}_t$ | 0.930 | 0.121 | 0.545 | 1.000 | 1.001 | 30,000 |
| $\hat{S}_c$ | 0.116 | 0.017 | 0.072 | 0.145 | 1.001 | 26,000 |
| $\hat{p}_t^{1\|1}$ | 0.779 | 0.031 | 0.731 | 0.860 | 1.001 | 30,000 |
| $\hat{p}_t^{2\|1}$ | 0.175 | 0.241 | 0.001 | 0.873 | 1.001 | 15,000 |
| $\hat{p}_t^{2\|2}$ | 0.354 | 0.019 | 0.317 | 0.392 | 1.001 | 30,000 |
| $\hat{\psi}_t^{1,2}$ | 0.163 | 0.015 | 0.135 | 0.194 | 1.001 | 6,900 |
| Deviance | 5,451.194 | 229.224 | 5,004.75 | 5,860.076 | 1.001 | 30,000 |

The mean uncorrected monthly probability of survival was 0.837 (95% credible interval [CRI] = 0.806–0.865) according to the MS model used to estimate Grass Carp survival in Lake Gaston (Figure 3a). This resulted in an uncorrected annual survival probability of 0.120 (95% CRI = 0.075–0.176; Figure 3c). By comparison, mean corrected monthly survival of Grass Carp was estimated to be 0.883 (95% CRI = 0.855–0.928; Figure 3b), resulting in a mean corrected annual survival probability of 0.233 (95% CRI = 0.152–0.406; Figure 3d).

The posterior distributions of the difference between corrected and uncorrected survival estimates (monthly and annual estimates) did not include zero in the 95% CRIs (Figure 4), indicating that bias resulting from the omission of state misclassification was statistically significant. Although the corrected and uncorrected monthly survival probability estimates differed by a mean of only 0.047 (95% CRI = 0.032–0.089), this difference was compounded when extrapolated throughout the year. The result was an estimated difference of 0.113 (95% CRI = 0.068–0.278) between corrected and uncorrected estimates of annual survival probability, indicating that survival was underestimated by 49% when not corrected for state misclassification.

The expected annual survival of tagged Grass Carp was estimated at 0.69 (95% CI = 0.52–0.78) based on fish length and the use of parameters from the inverse von Bertalanffy growth function and the life history-based survival estimator (Chen and Watanabe 1989). This estimate of annual survival was substantially higher (increase = 0.45) than the annual survival estimate from the telemetry model, even when accounting for state misclassification.

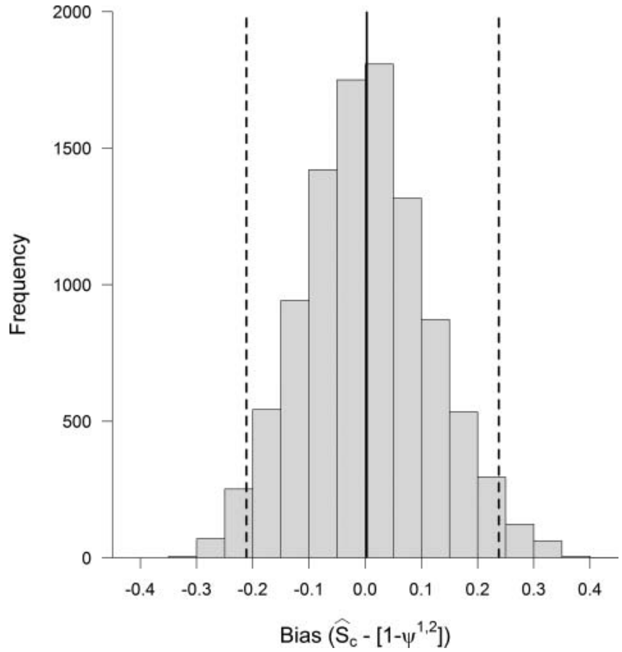


FIGURE 2. Histogram of estimated bias associated with the multistate mark–recapture model of Grass Carp poststocking survival; bias was calculated as the difference between the model-estimated value of corrected monthly survival ($\hat{S}_c$) and the true value of survival ($1 - \psi_t^{1,2}$) that was used to simulate capture histories for the analysis. The solid vertical line (black) represents the posterior mean; the dashed vertical lines represent the 95% credible interval.

## DISCUSSION

Our results clearly demonstrate that survival estimates for tagged Grass Carp can include substantial negative bias due to uncertainty in state assignment in MS survival models. Specifically, the assumption of zero error in the assignment of mortality to periodically sedentary tagged fish leads to underestimation of survival rates in fish that (1) remain still for long periods of time and (2) cannot be physically recovered or observed after apparent death. This problem has previously been shown in MS mark–recapture and occupancy models for other species (Nichols et al. 2007; Kendall 2009). In the case of fish telemetry, the usual inability to directly observe the mortality of tagged individuals has long been a concern (Hightower et al. 2001), but no solution to this problem has been proposed until now. Technology and methodologies for estimating survival from fish that exhibit periodic quiescence simply did not exist; however, methods for addressing state uncertainty are actively being developed (see Kendall 2009; Kendall et al. 2012). The model developed in the present study provides a useful starting point to account for a pervasive problem in estimating survival of Grass Carp and other animals from telemetry-based mark–recapture methods. This method has the ability to provide information over relatively short time frames (weeks or months), whereas several years of data collection are required for reliable estimation of fish survival from other methods, such as catch curve analysis (Morrow et al. 1997) or life history-based methods (Stich et al. 2013). The model developed here is also easily extended to include survival covariates and seasonal variation (see Kéry and Schaub 2012) and would serve as a useful tool for studying management decisions (e.g., stocking locations or dates) on an interim basis in adaptive management plans.

Our model provides a solution to the misclassification of live and dead states in Grass Carp and other species. For example, the utility of mortality sensors in tracking Bull Trout *Salvelinus confluentus* is uncertain because of the tendency of these fish to remain stationary for long periods (Watry and Scarnecchia 2008). Studies have also reported sedentary behavior in catfishes (e.g., Shroyer 2011) and reef fishes (e.g., Gell and Roberts 2003; Marshall et al. 2011). The gray literature is replete with examples in which researchers report uncertainty in the estimated survival of fish and wildlife species alike (e.g., Millsap et al. 2002), although most of these studies are not published—possibly as a result of difficulties in estimating demographic rates due to uncertainty in the rate of false positives in mortality sensors. In such situations, estimating the survival of periodically sedentary individuals from telemetry data can be confounded by the inability to reliably assign death based on telemetry tools and movement patterns. In the past, when the live or dead status of an individual could not be determined, estimation of survival from telemetry required either (1) making untestable and potentially unreliable assumptions or (2) "bracketing" survival estimates by running separate models that assumed those animals with uncertain fate were all dead or all alive (e.g., Heisey and Fuller 1985). Both of these methods reduce bias in survival estimates but at the cost of decreased precision in the estimates. Our model has the potential to be used in such situations and reduces the tradeoff in precision.

The present results demonstrate that continued monitoring of fish after they are initially assigned to the "dead" state can improve the estimation of demographic parameters. Accurate estimation of these parameters can be critical to the design of an effective adaptive management program, particularly when serial stocking of fish is used to fine-tune management strategies. A permanent state assignment (to a dead state) that is made based on remote indications of mortality from biotelemetry tools such as radio tags is perhaps too restrictive for use in mark–recapture models unless the dead animal can be recovered or unless there is other strong evidence that the animal has actually died (e.g., tag recovery). Grass Carp exemplify the uncertainty in assignment of live and dead states in telemetry studies, so our experiences with Lake Gaston Grass Carp are likely transferable to animals exhibiting similar behavior.

Without extended post-"mortality" observations for many of the fish in our study, survival models would have severely underestimated the annual survival rates that are used to inform stocking decisions. Estimates from fall 2013 indicate

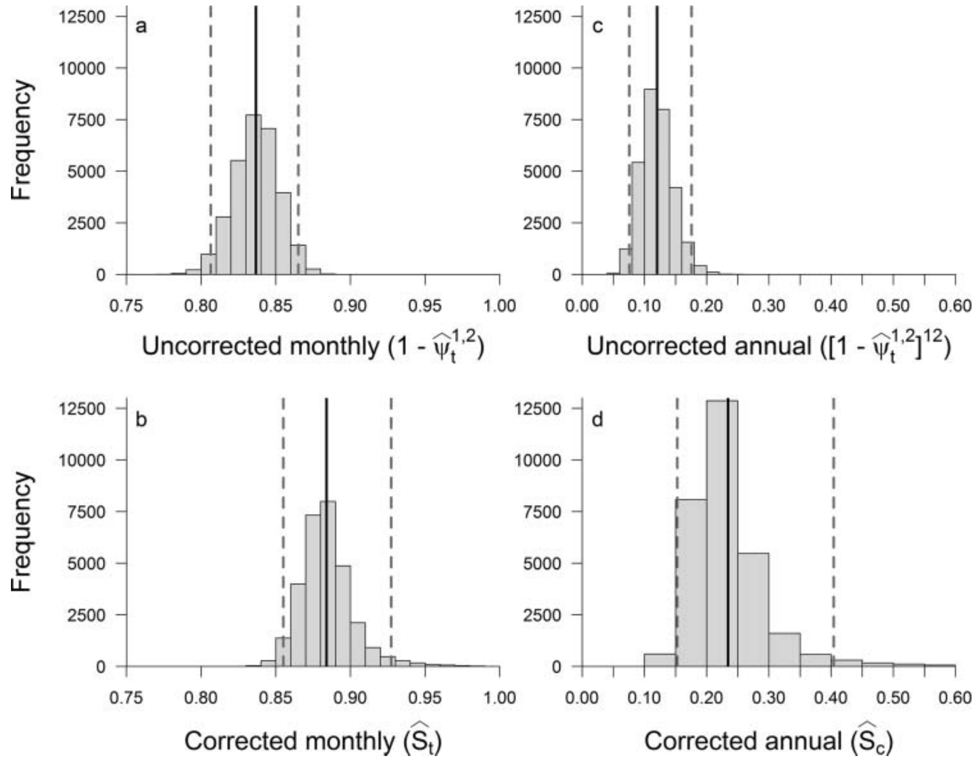


FIGURE 3. Histograms of posterior distributions for **(a)** uncorrected monthly survival ($1 - \psi_t^{1,2}$), **(b)** corrected monthly survival ($\hat{S}_t$), **(c)** uncorrected annual survival ($\left[1 - \psi_t^{1,2}\right]^{12}$), and **(d)** corrected annual survival ($\hat{S}_c$) of Grass Carp. Solid vertical lines (black) represent the posterior means; dashed vertical lines (gray) represent the 95% credible interval.

that hydrilla coverage was within 100 ha of target levels established in the weed management plan for Lake Gaston (ReMetrix 2014). Bias such as that observed in the uncorrected estimates of annual survival from the model in our study could have drastic effects on weed management efforts that seek to avoid complete eradication of submersed aquatic vegetation and that otherwise might be successful. If managers were to rely on negatively biased estimates of survival, overstocking of Grass Carp in the system could occur, potentially leading to the complete eradication of vegetation.

One potential concern with our approach is that the apparent "resurrection" of dead fish may be due to predation or scavenging. The movement patterns we observed were consistent with a well-documented behavioral syndrome of Grass Carp, which has been observed in other studies (Bain et al. 1990; Chilton and Poarch 1997). We suspect that a scavenged transmitter would only be mobile (within a predator or scavenger) for a short time before being expelled with feces. Such a scenario would result in fish that appear to be resurrected only once and over the relatively short period (i.e., days) typical of digestion time in fishes. For studies in which the scavenging of carcasses is a critical concern (e.g., Larsen et al. 2010), advances in telemetry technology (e.g., physiological sensor tags or depth tags) and data analysis (e.g., Romine et al. 2014) might provide solutions to this difficulty, with the former incurring a greater financial investment.

Our results suggest that tag shedding by Grass Carp (Schramm and Black 1984; Clapp et al. 1993; Prentice et al. 2000) has the potential to negatively bias survival estimates despite advances in telemetry, such as the miniaturization of tags (Cooke et al. 2013). The length-based survival estimated for tagged Grass Carp in this study was higher than the survival estimated for the same fish based on telemetry methods. It is worth noting, however, that the length-based estimator of Chen and Watanabe (1989) used in this study also is a model with its own assumptions and was empirically derived from a wide range of species that did not include Grass Carp. The Chen and Watanabe (1989) model assumes an inherent tradeoff between growth and longevity as a theoretical underpinning. In many ways, triploid Grass Carp differ from other fish used in the development of that estimator, particularly in terms of their long life span and fast growth. Future work may be necessary to quantify the degree of tag shedding or tag-related mortality in Grass Carp over extended periods if annual survival is to be estimated from telemetry data. Estimates of tag retention rate could be incorporated directly into the model structure presented here. This could be accomplished by deterministically adjusting survival estimates by known rates of tag shedding (sensu Sandstrom et al. 2013) or including tag shedding as a parameter within mark–recapture models. Incorporating prior information about monthly survival from previous studies (e.g., Kirk et al. 2000) would result in less bias from

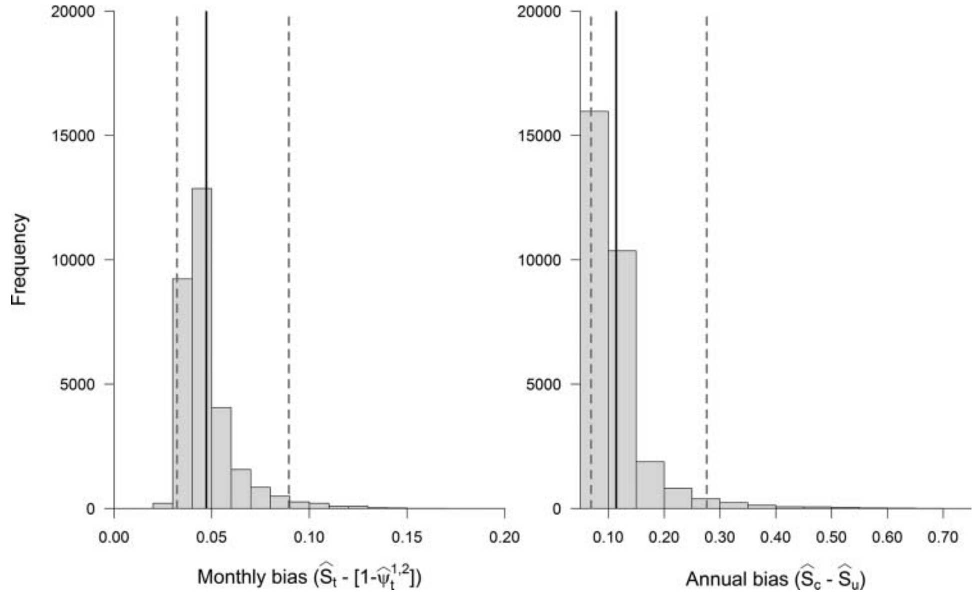


FIGURE 4. Histograms of differences between corrected ($\hat{S}_t$) and uncorrected ($1 - \psi_t^{1,2}$) estimates of monthly survival probability (left panel) and between corrected ($\hat{S}_c$) and uncorrected ($\left[1 - \psi_t^{1,2}\right]^{12}$) estimates of annual survival probability (right panel) for Grass Carp. Solid vertical lines (black) represent the means; dashed vertical lines (gray) represent the 95% credible interval.



tag shedding or tag-related mortality. For studies of other species with higher rates of tag retention, such violations of model assumptions may not be as great a concern. Addressing the issue of tag shedding will, by all accounts, be trivial in comparison with the problems arising from state misclassification.

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## REFERENCES


Allen, S. K. Jr., and R. J. Wattendorf. 1987. Triploid Grass Carp: status and management implications. Fisheries 12(4):20–24.

Bain, M. B., D. H. Webb, M. D. Tangedal, and L. N. Mangum. 1990. Movements and habitat use by Grass Carp in a large mainstream reservoir. Transactions of the American Fisheries Society 119:553–561.

Bonar, S. A., S. A. Vecht, C. R. Bennett, G. B. Pauley, and G. L. Thomas. 1993. Capture of Grass Carp from vegetated lakes. Journal of Aquatic Plant Management 31:168–174.

Chen, S., and S. Watanabe. 1989. Age dependence of natural mortality coefficient in fish population dynamics. Nippon Suisan Gakkaishi 55:205–208.

Chilton, E. W. II, and S. M. Poarch. 1997. Distribution and movement behavior of radio-tagged Grass Carp in two Texas reservoirs. Transactions of the American Fisheries Society 126:467–476.

Clapp, D. F., R. S. Hestand III, and B. Z. Thompson. 1994. Hauling and poststocking mortality of triploid Grass Carp. Journal of Aquatic Plant Management 32:41–43.

Clapp, D. F., R. S. Hestand III, B. Z. Thompson, and L. L. Connor. 1993. Movement of triploid Grass Carp in large Florida lakes. North American Journal of Fisheries Management 13:746–756.

Colle, D. E, J. V. Shireman, R. D. Gasaway, R. L. Stetler, and W. T. Haller. 1978. Utilization of selected removal of Grass Carp (*Ctenopharyngodon idella*) from an 80-hectare Florida lake to obtain a population estimate. Transactions of the American Fisheries Society 107:724–729.

Cooke, S. J., J. D. Midwood, J. D. Thiem, P. Klimley, M. C. Lucas, E. B. Thorstad, J. Eiler, C. Holbrook, and B. C. Ebner. 2013. Tracking animals in freshwater with electronic tags: past, present, and future. Animal Biotelemetry [online serial] 1:5.

Devineau, O., T. M. Shenk, G. C. White, P. F. Doherty Jr., P. M. Lukacs, and R. H. Kahn. 2010. Evaluating the Canada lynx reintroduction programme in Colorado: patterns in mortality. Journal of Applied Ecology 47:524–531.

Devineau, O. T., W. L. Kendall, P. F. Doherty, T. M. Shenk, G. C. White, P. M. Lukacs, and K. P. Burnham. 2014. Increased flexibility for modeling telemetry and nest-survival data using the multistate framework. Journal of Wildlife Management 78:224–230.

Gell, F. R., and C. M. Roberts. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. Trends in Ecology and Evolution 18:448–455.

Heisey, D. M., and T. K. Fuller. 1985. Estimation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Hightower, J. E., J. R. Jackson, and K. E. Pollock. 2001. Use of telemetry methods to estimate natural and fishing mortality of Striped Bass in Lake Gaston, North Carolina. Transactions of the American Fisheries Society 130:557–567.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–247.

Kendall, W. L. 2009. One size does not fit all: adapting mark–recapture and occupancy models for state uncertainty. Pages 765–780 *in* D. L. Thomson, E. G. Cooch, and M. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York.

Kendall, W. L., G. C. White, J. E. Hines, C. A. Langtimm, and J. Yoshizaki. 2012. Estimating parameters of hidden Markov models based on marked individuals: use of robust design data. Ecology 93:913–920.

Kenward, R. 2001. A manual for wildlife radio tagging. Academic Press, San Diego, California.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, San Diego, California.

Kirk, J. P., K. J. Killgore, J. V. Morrow Jr., S. D. Lamprecht, and D. W. Cooke. 2001. Movements of triploid Grass Carp in the Cooper River, South Carolina. Journal of Aquatic Plant Management 39:59–62.

Kirk, J. P., J. V. Morrow Jr., K. J. Killgore, S. J. De Kozlowski, and J. W. Preacher. 2000. Population response of triploid Grass Carp to declining levels of hydrilla in the Santee Cooper reservoirs, South Carolina. Journal of Aquatic Plant Management 38:14–17.

Kruschke, J. K. 2011. Doing Bayesian data analysis: a tutorial with R and BUGS. Academic Press, San Diego, California.

Lake Gaston Stakeholders Board. 2005. Managing aquatic plants in Lake Gaston, a long term action plan. Available: http://www.lgaston.org/Stakeholders/Plan.pdf. (January 2014).

Larsen, R. T., D. F. Bentley, and J. T. Flinders. 2010. Implications of woodrats and other scavengers for avian telemetry studies. Journal of Wildlife Management 72:1152–1155.

Maceina, M. J., J. W. Slipke, and J. M. Grizzle. 1999. Effectiveness of three barrier types for confining Grass Carp in embayments of Lake Seminole, Georgia. North American Journal of Fisheries Management 19:968–976.

Mackay, D., and J. Moreau. 1990. A note on the inverse function of the von Bertalanffy growth function. ICLARM (International Center for Living Aquatic Resources Management) Fishbyte 8:28–31.

Mackenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutiérrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. Ecology 90:823–835.

Marshall, A., J. S. Mills, K. L. Rhodes, and J. McIlwain. 2011. Passive acoustic telemetry reveals highly variable home range and movement patterns among Unicorn Fish within a marine reserve. Coral Reefs 30:631–642.

Millsap, B., T. Breen, E. McConnell, T. Steffer, L. Phillips, N. Douglass, and S. Taylor. 2002. Comparative fecundity and survival of bald eagles fledged from suburban and rural natal areas. Florida Fish and Wildlife Commission, Final Performance Report, Tallahassee.

Morrow, J. V. Jr., J. P. Kirk, and K. J. Killgore. 1997. Collection, age, growth, and population attributes of triploid Grass Carp stocked into the Santee–Cooper reservoirs, South Carolina. North American Journal of Fisheries Management 17:38–43.

Nichols, J. D., J. E. Hines, D. I. Mackenzie, M. E. Seamans, and R. J. Gutiérrez. 2007. Occupancy estimation and modeling with multiple states and state uncertainty. Ecology 88:1395–1400.

Pine, W. E., K. H. Pollock, J. E. Hightower, T. J. Kwak, and J. A. Rice. 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries 28(10):10–23.

Pollock, K. H., C. M. Bunck, S. R. Winterstein, and C. L. Chen. 1995. A capture–recapture survival analysis model for radio-tagged animals. Journal of Applied Statistics 22:661–672.

Pollock, K. H., S. R. Winterstein, and M. J. Conroy. 1989. Estimation and analysis of survival distributions for radio-tagged animals. Biometrics 45:99–109.

Prentice, J. A., W. J. Dean Jr., M. S. Reed, and E. W. Chilton II. 2000. Movement of triploid Grass Carp among small hydropower impoundments of the Guadalupe River, Texas. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 52(1998):49–61.

R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

ReMetrix. 2014. Lake Gaston 2013 submerged vegetation mapping summary report. ReMetrix LLC, Carmel, Indiana. Available: http://www.imembersdb.com/Accounts/2007/Treatments_and_Surveys//Remetrex%202013%20Survey%20Report.pdf. (June 2014).

Richardson, R. J. 2008. Aquatic plant management and the impact of emerging herbicide resistance issues. Weed Technology 22:8–15.

Romine, J. G., R. W. Perry, S. V. Johnston, C. W. Fitzer, S. W. Pagliughi, and A. S. Blake. 2014. Identifying when tagged fishes have been consumed by piscivorous predators: application of multivariate mixture models to movement parameters of telemetered fishes. Animal Biotelemetry 2:1–13.

Ryan, F. J., C. R. Coley, and S. H. Kay. 1995. Coexistence of monoecious and dioecious hydrilla in Lake Gaston, North Carolina and Virginia. Journal of Aquatic Plant Management 33:8–12.

Sandstrom, P. T., A. J. Ammann, C. Michel, G. Singer, E. D. Chapman, S. Lindley, R. B. MacFarlane, and A. P. Klimley. 2013. Growth, survival and tag retention of steelhead trout (*Oncorhynchus mykiss*) and its application to survival estimates. Environmental Biology of Fishes 96:145–164.

Schramm, H. L. Jr., and D. J. Black. 1984. Anesthesia and surgical procedures for implanting radio transmitters into Grass Carp. Progressive Fish-Culturist 46:185–190.

Schramm, H. L. Jr., and K. J. Jirka. 1986. Evaluation of methods for capturing Grass Carp in agricultural canals. Journal of Aquatic Plant Management 24:57–59.

Seber, G. A. F. 1965. A note on the multiple recapture census. Biometrika 52:249–259.

Shroyer, S. M. 2011. Movement and site fidelity of Flathead Catfish in the Minnesota River. Pages 473–483 *in* P. H. Michaletz and V. H. Travnichek, editors. Conservation, ecology and management of catfish: the second international symposium. American Fisheries Society, Symposium 77, Bethesda, Maryland.

Stich, D. S., V. DiCenzo, E. F. Frimpong, Y. Jiao, and B. R. Murphy. 2013. Growth and population size of Grass Carp incrementally stocked for biological control. North American Journal of Fisheries Management 33:14–25.

Stott, B., and I. C. Russell. 1979. An estimate of a fish population which proved to be wrong. Fisheries Management 10:169–171.

Thorstad, E. B., A. H. Rikardsen, A. Alp, and F. Okland. 2013. The use of electronic tags in fish research: an overview of fish telemetry methods. Turkish Journal of Fisheries and Aquatic Sciences 13:881–896.

Vetter, E. F. 1988. Estimation of natural mortality in fish stocks: a review. U.S. National Marine Fisheries Service Fishery Bulletin 86:25–43.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. Human Biology 10:181–213.

Watry, C. B., and D. L. Scarnecchia. 2008. Adfluvial and fluvial life history variations and migratory patterns of a relict charr, *Salvelinus confluentus*, stock in west-central Idaho, USA. Ecology of Freshwater Fish 13:231–243.

Winter, J. D. 1996. Advances in underwater biotelemetry. Pages 555–585 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.