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ARTICLE

Simulated Use of YY Male Stocking and Suppression for Eradicating Common Carp Populations

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Abstract

The introduction and subsequent spread of Common Carp *Cyprinus carpio* throughout the world represent one of the most destructive and pervasive forces impacting aquatic ecosystems. Herein we use computer simulations to predict if stocking YY male carp in conjunction with manual netting or piscicide use could eradicate invasive Common Carp populations. Two forms of YY males were evaluated, including sperm-producing (M_{YY}) and egg-producing (F_{YY}) fish. A stochastic individual-based population model was used to evaluate the effects of simulated management actions on both the abundance and extirpation probabilities of high- and low-density populations. Results predicted that some YY male stocking scenarios alone could eradicate carp populations. For example, when stocking F_{YY} carp into low-density populations, predicted extirpation probabilities exceeded 0.87 when stocking at least 50 carp/ha was maintained for at least 10 years. Additionally, a one-time use of rotenone (to reduce the virtual population by 90%) plus stocking at least 50 F_{YY} carp/ha for at least 5 years into low-density populations resulted in predicted extirpation probabilities exceeding 0.88. Favorable extirpation probabilities were also obtained by combining YY male stocking and either selective (i.e., no culling of stocked YY males) or non-selective annual suppression. For example, F_{YY} stocking with only 10% sustained, non-selective suppression yielded extinction probabilities exceeding 95% in 15 years, while increasing suppression levels to 50% resulted in extirpation probabilities over 95% within 5 years. Without exception, M_{YY} stocking functioned far less efficiently in simulations than F_{YY} stocking, but M_{YY} carp did work in a small subset of low-density scenarios and may also have prophylactic utility where prior eradication has occurred and where there is a high risk of re-invasion. We conclude that stocking of YY male Common Carp is worthy of field testing, but additional simulations are needed to explore other questions not addressed in this study.

Importation of Common Carp *Cyprinus carpio* in North America was begun by several private individuals in the mid-1800s, with broad distribution first undertaken in the 1880s by the U.S. Fish Commission, precursor to the U.S. Fish and Wildlife Service. For example, in 1883, the agency distributed 260,000 Common Carp to 9,872 individual applicants whose requests originated from 99% of existing U.S. congressional districts (Fritz 1987). Given such widespread introduction, the fish rapidly spread across the continent, a scenario repeated in nearly every region of the globe, making the Common Carp one of the most detrimental of all plant or animal invasives worldwide (Global Invasive Species Database 2019).

Outside its native range, the Common Carp is very disruptive to aquatic habitat due to its method of feeding, which uproots macrophytes and stirs up sediments, both of which typically result in drastic increases in turbidity. This was first reported by Cahn (1929), who also noted commensurate negative effects on game fish. A host of subsequent studies has documented Common Carp impacts and further clarified food web shifts, water quality declines, and game fish reductions (reviewed by Weber and Brown 2009). In short, most waters invaded by Common Carp are transformed to a turbid-water state, with fish assemblages containing few sight-feeding predators—the feeding method of nearly all North American sport fish (Jackson et al. 2010).

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Accordingly, Common Carp have been targeted for control on multiple continents for nearly a century (e.g., Burr 1931; Ricker and Gottschalk 1941; Rose and Moen 1953; King and Hunt 1967; Bulow et al. 1988; King et al. 1997; Taylor et al. 2012). Based on a summary of 23 such suppression studies, it has been noted that Common Carp control is logistically difficult, expensive, time consuming, and often unsuccessful (Weber and Brown 2009). For example, in one of the longest-running removal efforts conducted solely by governmental agency personnel in the USA (11 years), annual biomass removal by netting of Bigmouth Buffalo *Ictiobus cyprinellus* declined markedly in East Okoboji Lake, Iowa, but similar declines were not apparent for Common Carp (Rose and Moen 1953).

Common Carp are often targeted with piscicides such as rotenone, but “rough fish” control using such chemicals is far from certain, with only 48% of 92 treatments considered successful by participants, though published estimates of total kill efficiency are rare (Meronek et al. 1996). One whole-lake rotenone project targeting Common Carp reported that 75% of the carp population was killed (Shrage and Downing 2004). Because of the difficulty in obtaining their complete eradication, Common Carp removal programs often contain biomass suppression targets, typically 50 or 100 kg/ha, the attainment of which is believed to improve water quality and improve ecosystem function (Brown and Gilligan 2014; Lechelt and Bajer 2016; Pearson et al. 2019).

Despite the past focus on manual removal or piscicides for invasive fish control, such efforts alone are often ineffective at completely eradicating many invasive populations because at least a few fish survive to restart and rapidly regrow the exotic population (Meronek et al. 1996; Makhrov et al. 2014). In the case of Common Carp, this ability to re-populate is magnified by extremely high fecundity, with a single adult female producing up to 3 million eggs (Sorensen and Bajer 2011) and fecundities often averaging between 500,000 and 750,000 (Sivakumaran et al. 2003; Bajer and Sorensen 2010).

Given the poor success of past suppression efforts, interest in invasive carp management over the last few decades has shifted from manual removal or piscicide application alone to an integrated pest management (IPM) approach involving the concurrent use of multiple suppression/control methods (Kogan 1998; Bajer and Sorensen 2010; Sorensen and Bajer 2011). Several field efforts have demonstrated positive results from IPM programs (Iowa Department of Natural Resources 2012; Taylor et al. 2012; Bartodziej et al. 2017), though the resources and sustained agency focus for such undertakings appear daunting (e.g., Havranek et al. 2019).

Recent interest in Common Carp IPM has also included population simulations where both eradication probabilities and the ability to attain the population biomass reduction targets noted above are tracked. For example, Brown and Gilligan (2014) simulated a suite of carp control measures, including various manual removal approaches, release of the cyprinid herpesvirus-3, and use of a genetic “daughterless” transgenic construct. Observed effects were small; complete eradication was not achieved, and program biomass targets were not met. However, combination of the two novel approaches with traditional manual suppression methods was not assessed. More recently, a suite of IPM Common Carp control measures was assessed via simulation for Malheur Lake, a shallow lake–wetland system in southeast Oregon. The combination of several active removal methods targeting both juvenile and adult Common Carp was predicted to reduce biomass below an a priori threshold target of 50 kg/ha (Pearson et al. 2019), though the authors stated it would be unrealistic to maintain the requisite exploitation levels necessary over sufficiently long time scales. Despite the authors’ conclusion, the Pearson et al. (2019) study confirmed that not only must the adult portion of carp populations be suppressed, but juvenile recruitment also must be controlled, an observation noted previously by Weber and Brown (2009).

The Trojan Y chromosome (TYC) method represents such a potential recruitment suppression tool. First conceived by John Teem (Mills 2009) and subsequently described in two papers (Gutierrez and Teem 2006; Teem and Gutierrez 2010), this approach is so named because it involves a second, “hidden” Y chromosome present in stocked individuals. In the originally described approach, feminized fish (egg-producing fish with two Y chromosomes; F_{YY}) are produced by common commercial aquaculture practices involving selective breeding and hormonal sex-reversal (Cotton and Wedekind 2007). The F_{YY} fish are released into an invasive fish population, where they subsequently mate with normal males, giving rise to all-male progeny, half of which would be sperm-producing YY males (M_{YY}), further speeding the extirpation process (Gutierrez and Teem 2006; Teem and Gutierrez 2010). A variant of the original TYC concept is to release M_{YY} fish—an approach that, although expected to be less efficient, has also been shown to be effective for eradicating invasive populations in model simulations (Parshad 2011; Schill et al. 2017). Both studies suggested M_{YY} stocking to be more practical because of the technical difficulties involved in feminizing large numbers of progeny before release (Teem et al. 2020). Regardless of the type of YY fish (F_{YY} or M_{YY}) being released, the proportion of males in the population theoretically increases over time until females are eventually eliminated entirely, causing population extirpation upon stocking cessation.

Publication of early TYC (hereafter, "YY male") papers stimulated an array of subsequent simulation studies addressing a host of questions using complex mathematical formulae (e.g., Parshad and Gutierrez 2010; Gutierrez et al. 2012; Parshad et al. 2013; Wang et al. 2014; Kelly and Wang 2017; Lyu et al. 2019; Beauregard et al. 2020). However, scant investigation has been devoted to combining manual suppression with the stocking of YY male fish (but see Schill et al. 2017 and Day et al. 2020) or to comparing the efficacy of the original F_{YY} stocking approach to M_{YY} stocking in hypothetical IPM programs (but see Kelly and Wang 2017). In this study, we used a stochastic simulation model to predict whether stocking YY male carp in conjunction with manual or piscicide suppression of wild fish would likely eradicate undesirable Common Carp populations. Specific objectives were to (1) estimate the likelihood of and years to achieve eradication of virtual Common Carp populations using various levels of either F_{YY} or M_{YY} stocking; (2) determine how much concurrent suppression of the wild population via manual removal or piscicide use would influence the likelihood of and years to achieve eradication; and (3) estimate population biomass before, during, and after YY male stocking for a number of management scenarios.

METHODS

Model description.— A stochastic individual-based population model (Grimm and Railsback 2005), similar to the model used by Brown and Walker (2004), was used to evaluate the effects of simulated management actions (i.e., YY male stocking, manual netting suppression, and rotenone treatment) on the abundance and extirpation probability of Common Carp for two simulated populations (high density and low density; see below). Most input values for parameters in the model were derived from sampling of Common Carp in Lake Lowell, Idaho, in 2010 (Kozfkay et al. 2011), though some parameters were not available and were instead obtained from the literature (Table 1).

In the individual-based population model, individuals were added to the virtual population through a simulated recruitment process that was a function of the number of spawners. To become a spawner, immature individuals underwent stochastic growth, maturity, and mating processes. Additionally, F_{YY} and M_{YY} individuals were added to the population through external stocking. Individuals were removed from the virtual population through a simulated natural mortality process along with management actions that included simulated mechanical or chemical suppression.

The number of natural age-0 recruits added to the virtual population at time t (R_t) in the model was simulated using a Ricker stock–recruitment function (Ricker 1954):

$$R_t = \alpha S_t e^{-\beta S_t} + \varepsilon_t,$$

where S_t is the number of spawners in the population at time t, α and β are the parameters of the Ricker model, and ε_t is an additive random normal variable with a mean of zero and a SD that was 0.25 times the adult equilibrium abundance. The random variable allowed for variation in recruitment. Abundance and recruitment were simulated on a per-hectare basis (Brown and Walker 2004; Brown and Gilligan 2014). The α parameter in the Ricker function represents the slope of the recruitment line at the origin and is proportional to fecundity. The β parameter represents the rate of decline in recruitment as spawner abundance increases (i.e., density dependence). The input value for α used in the simulation was 8.004 and was obtained from Koehn et al. (2000). This value suggests that spawners produce 8.004 age-0 recruits when they are unaffected by negative density-dependent effects. Two values for β were used in the simulation that ultimately resulted in two equilibrium population sizes (Table 1; Figure 1). Similar to the α parameter, the first β value was also from Koehn et al. (2000) and was 0.008. This value resulted in a carrying capacity of 368 recruits/ha (hereafter, "high-density" population). The resulting adult population density was similar to what was estimated at Lake Lowell at the time of sampling (Kozfkay et al. 2011) but was larger than any density observed by Bajer and Sorensen (2012). Therefore, to simulate a lower-density population, the β parameter was adjusted to 0.0352, which resulted in a carrying capacity of 84 recruits/ha (hereafter, "low-density" population).

For the purpose of the stock–recruitment model, it was assumed in the simulation that each mature fish in the population spawned successfully if it was paired with a mate on an annual, discrete basis. Thus, in the simulation, the number of spawners may have differed from the number of mature individuals in the population, particularly when sex ratios were shifted towards males, as some males may not have successfully fertilized eggs. Additionally, under the base model (i.e., no F_{YY} or M_{YY} carp stocking) each recruit was assigned a sex with probability of 0.5 with binomial variation (i.e., a 50:50 sex ratio).

Length of individual i at age T (l_i) in the model was simulated using a von Bertalanffy growth function (Beverton and Holt 1957):

$$l_i = L_\infty\left[1 - e^{-K(T-t_0)}\right] + \varepsilon_i,$$

where L_∞, K, and t_0 are parameters of the growth model and ε_i is a normal random variable with a mean of zero and a SD of 30. All growth parameters were estimated

TABLE 1. Input parameters used in the individual-based model to evaluate the effect of management actions on Common Carp abundance.

Parameter	Value	Source
	Mortality	
A	0.43	Kozfkay et al. (2011)
	Ricker stock–recruitment function	
α	8.004	Koehn et al. (2000)
β	0.008, 0.0352	Koehn et al. (2000), Kozfkay et al. (2011)
ε_t	Mean = 0, SD = 0.25 × abundance	
	von Bertalanffy growth function	
L_∞	610	Kozfkay et al. (2011)
K	0.336	Kozfkay et al. (2011)
t_0	0	Kozfkay et al. (2011)
ε_i	Mean = 0, SD = 30	Kozfkay et al. (2011)
	Maturity and selectivity	
Lm50	217	Brown and Walker (2004)
Lm95	308	Brown and Walker (2004)
	Length–weight	
d	$e^{-9.987}$	Kozfkay et al. (2011)
b	2.784	Kozfkay et al. (2011)
ε_i	Mean = 0, SD = 1.06	Kozfkay et al. (2011)

using data from Common Carp sampled in Lake Lowell (Table 1; Figure 1). It was assumed that males and females had the same growth rate.

The probability of maturity of individual i at length l_i (pr[m_i]) was modeled as a function of an individual's length:

$$\mathrm{pr}(m_i) = \frac{1}{\{1 + e^{\log_e[(19)(l_i - \mathrm{Lm50})/(\mathrm{Lm50} - \mathrm{Lm95})]}\}},$$

where Lm50 and Lm95 represent the length (mm) at which 50% and 95% of individuals are sexually mature, respectively. Input values in the simulation for Lm50 and Lm95 were 217 and 308 mm, respectively (Table 1; Figure 1). These values were based on length-at-age values from Brown and Walker (2004) but were altered based on the growth model for Lake Lowell Common Carp (which were faster growing than those in the Brown and Walker [2004] study) such that the parameters represent the same age at maturity rather than length at maturity. At each time step, for each individual, a binomial trial was conducted with probability pr(m_i), such that a success would indicate that individual i was sexually mature, with resulting binomial error in maturity. It was assumed that males and females matured at the same rate. A sensitivity analysis was conducted to evaluate the sensitivity of the effectiveness of simulated management actions to changes in maturity parameters (see Appendix Figure A.1). It was assumed that all mature fish successfully spawned each year if they were paired with a mate.

The weight of individual i (W_i) was modeled as a function of length using the equation:

$$W_i = d l_i^b e^{\varepsilon_i},$$

where d and b are parameters of the length–weight model and ε_i is a multiplicative normal random variable with a mean of zero and an SD of 1.06. Parameters for the length–weight model were estimated using data from Common Carp sampled in Lake Lowell (Table 1; Figure 1). It was assumed that males and females had the same length–weight relationship.

The input value for annual natural mortality (A) of fish older than age 0 in the simulation was 0.43 (Table 1; Figure 1). This value was based on a catch curve analysis from the Lake Lowell carp sample (Kozfkay et al. 2011). It was assumed that all individuals (e.g., males and females, all ages) underwent the same annual natural mortality process. Similar to maturity, at each time step a binomial trial was conducted (with probability [1.00 − 0.43]), in which a success indicated that the individual would survive the year, with binomial error. If an individual did not survive from one year to the next, that fish was removed from the population.

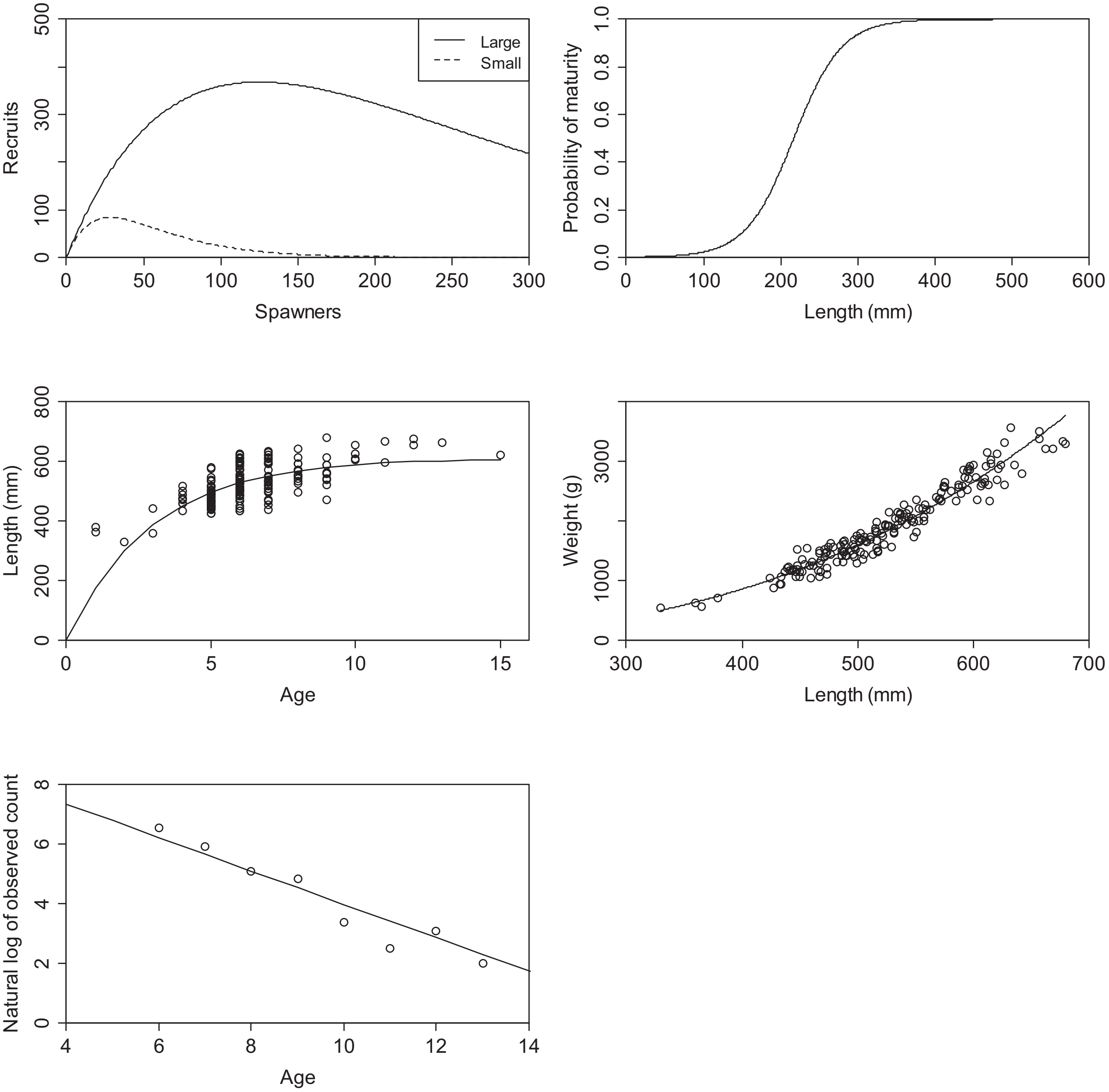

FIGURE 1. Input functions, including stock recruitment of high- and low-density populations (top left), maturity (top right), growth (middle left), weight (middle right), and mortality (catch curve; bottom left), used in the individual-based model to evaluate the effect of management actions on Common Carp populations.

Stochastic simulation model and management actions.— The model was initialized with 50 age-4 males and 50 age-4 females that were assumed to be sexually mature. Lengths and weights were randomly assigned using the functions and variability described above. The model progressed using annual time steps where the initialized population (and subsequent recruits) underwent mortality, growth, maturity, mating, spawning, and recruitment processes using the functions described above along with the associated stochasticity for each parameter. Under each simulated scenario, the initialized population was allowed to progress for 30 years before any simulated management actions (described below) were implemented and for 20 years after the management actions were ceased. The amount of time that each management action was applied varied from 1 to 45 years and was dependent on the management action.

In addition to the base individual-based population model (i.e., no management actions implemented), three general management actions were simulated. These included (1) stocking of F_{YY} or M_{YY} carp; (2) a whole-lake rotenone treatment (achieving a one-time 90% carp suppression rate), with and without annual stocking of F_{YY} and M_{YY} carp starting in the same year as the treatment; and (3) manual netting suppression of carp annually, with and without concurrent annual stocking of F_{YY} and M_{YY} carp. The F_{YY} and M_{YY} carp simulations were conducted independently (i.e., no situations were evaluated in which they were stocked concurrently).

F_{YY} and M_{YY} stocking.— Under the F_{YY} stocking management action, after allowing the initialized population to progress for 30 years, the number of simulated F_{YY} carp stocked included adding 25–1,000 F_{YY} carp/ha annually for 5–45 years at each stocking rate. Virtual F_{YY} carp were stocked at age 0 but after the breeding pulse of the natural carp population and were not assumed to undergo the same density-dependent processes as natural age-0 carp in the population. Thus, stocked age-0 carp survived the first year with probability $1 - A$, which was 0.57. This would mimic a scenario in which F_{YY} fish were stocked near the middle of their first year of life. It was assumed that F_{YY} carp were sexually immature, and each individual's length and weight were randomly assigned based on the length and weight models described above (Figure 1). It was also assumed that F_{YY} carp had the same growth and survival rate of carp in the natural population (other than age-0 carp). Additionally, it was assumed that production of natural age-0 carp was the same for F_{YY} and natural F_{XX} spawners, regardless of the sex of the male parent (i.e., M_{XY} or M_{YY}). For instance, if there were equal numbers of F_{YY} and F_{XX} spawners in the population, it was assumed that half of the recruits would be offspring of F_{YY} spawners and half would be offspring of F_{XX} spawners after the density-dependent process took place.

Although M_{YY} carp were not stocked concurrently with F_{YY} carp, when an F_{YY} carp spawns with a normal M_{XY} male, on average, 50% of their offspring are M_{YY} (Gutierrez and Teem 2006). Consequently, F_{YY} carp and F_{XX} carp can potentially spawn with M_{XY} or M_{YY} carp in future generations even when M_{YY} carp are not externally introduced. It was assumed in the simulation that female carp eggs were randomly fertilized by M_{XX} or M_{YY} carp in proportion to their relative abundance, with binomial variation. When an F_{YY} carp egg was fertilized by an M_{YY} carp, the resulting offspring was M_{YY} with a probability of 1. When an F_{YY} carp egg was fertilized by a normal male (M_{XY}), a binomial trial was conducted for each egg with probability 0.50 to determine whether the offspring was M_{YY} or M_{XY}. When a normal female (F_{XX}) egg was fertilized by an M_{YY} carp, the offspring was assumed to be M_{XY} with a probability of 1 (Kennedy et al. 2018), and when a normal female egg was fertilized by a normal male, a binomial trial was conducted with probability 0.50 to determine whether the offspring was a normal male or a normal female.

The simulated M_{YY} stocking scenario was similar to the F_{YY} stocking scenario in that the same stocking rates and time intervals were evaluated. Additionally, the same assumptions about growth, survival, and maturity for introduced M_{YY} carp were made as for F_{YY} carp. Although it was assumed that all F_{YY} carp were able to mate, this was not necessarily the case for M_{YY} carp if the number of males was greater than the number of females in the population. The probability of a female egg being fertilized by an M_{YY} carp was proportional to M_{YY} abundance relative to normal males, with binomial variation.

Rotenone and YY carp stocking.— In addition to the management actions of stocking F_{YY} and M_{YY} fish, a whole-lake rotenone treatment was simulated to evaluate its effectiveness at collapsing the Common Carp population. Under this scenario, the normal population was allowed to progress for 30 years. At year 31, a simulated one-time rotenone treatment was conducted, where it was assumed that 90% of all fish were removed from the population. Fish of all sizes were assumed equally vulnerable to the rotenone treatment, and fish that were removed were selected with equal probability. After the rotenone treatment, the population was monitored for 20 years and the extirpation probability was estimated. Additionally, scenarios were evaluated where F_{YY} and M_{YY} carp were stocked starting at year 31, after the one-time rotenone treatment was implemented. Simulated F_{YY} and M_{YY} carp were stocked at the same rate and frequency as the management action without the rotenone treatment (i.e., 25–1,000 F_{YY} or M_{YY} carp/ha for 5–45 years). The extirpation probability was estimated 20 years after the stocking of F_{YY} and M_{YY} carp concluded.

Suppression and YY carp stocking.— Simulated manual suppression, such as netting or seining (Ricker and Gottschalk 1941; Rose and Moen 1953; Gilligan et al. 2005), was also evaluated. Two variations of manual suppression were evaluated: one in which all fish, including normal carp and introduced F_{YY} and M_{YY} carp, were removed (i.e., unselective); and one in which stocked YY males were marked and only normal carp were removed (i.e., selective). Four levels of suppression were evaluated, where 10, 25, 50, and 75% of individuals susceptible to capture were removed. Subsequent scenarios were evaluated where F_{YY} or M_{YY} carp were stocked after suppression took place at the same rates and frequency as described above (except concurrent with the netting/seining suppression effort) as well as a scenario where manual suppression occurred but no F_{YY} carp or M_{YY} carp were introduced. The probability of a fish being captured during the simulated suppression effort was size selective to simulate gear selectivity. The probability that a fish would be captured was simulated using the same function, with the same parameters, as the maturity function. A binomial trial was conducted with a probability based on the maturity function for each fish of length l_i. If the binomial trial was a success, then that individual was considered susceptible to capture. The percentage of the population that was removed (i.e., 10–75%) was based only on individuals that were deemed susceptible to suppression through the binomial process. Natural and YY carp were assumed to have the same probability of capture.

For each management action, the virtual population was simulated 1,000 times. At each time step (i.e., year), the total number of fish per hectare, total number of adult fish per hectare (including the total number of each sex and chromosome type [F_{XX}, M_{XY}, M_{YY}, and F_{YY}]), sex ratio, and total biomass per hectare in the virtual population were recorded. A population was considered extirpated when the total number of individuals in the population was zero at the end of the simulation process, which included the initial untreated population (30 years), management action years (1–45 years), and after the management action ceased (20 years). Extirpation probability was estimated as the number of simulation iterations in which the population was extirpated at the end of the simulation divided by the total number of simulation iterations (i.e., 1,000). All analyses were conducted using R statistical software (R Development Core Team 2015).

RESULTS

The mean adult equilibrium abundance was 508 Common Carp/ha for the virtual high-density population and 150 fish/ha for the low-density population in the absence of management actions. The mean biomass of all carp was approximately 467 kg/ha for the virtual high-density population and 108 kg/ha for the low-density population. All simulated carp populations persisted when no management actions were implemented (i.e., extirpation probability was zero) over the duration of the simulations for both the high- and low-density populations.

F_{YY} and M_{YY} stocking.— Figure 2 illustrates the results for 2 of the 1,000 simulations that were run for the scenario of stocking 100 F_{YY} carp/ha for 10 years in a high-density Common Carp population, with no suppression of the wild population. In these two examples, one population persisted (left plots) and one was extirpated (right plots). In general, sex ratios of wild carp became highly skewed and abundance reached extremely low levels for all F_{YY} and M_{YY} stocking rates, even for populations that persisted. Abundance generally increased back to equilibrium abundance soon after YY male stocking was terminated unless the population was extirpated.

When stocking F_{YY} carp in the high-density population with no suppression, the probability of extirpation was less than 0.03 for all durations of stocking when only 25 F_{YY} carp/ha were stocked (Figure 3). However, extirpation probability in the high-density population rose rapidly and exceeded 0.95 if F_{YY} stocking density exceeded 200 F_{YY} carp/ha for at least 15 years, and extirpation probability approached 0.60 within only 10 years. For the low-density population, the probability of extirpation exceeded 0.87 with an F_{YY} stocking density of at least 50 F_{YY} carp/ha for at least 10 years. In contrast, the probability of extirpation was negligible for all M_{YY} stocking densities and durations in the high-density population. In the low-density population, the probability of extirpation using M_{YY} stocking did not exceed 0.50 until stocking occurred for at least 15 years at a density of at least 600 M_{YY} carp/ha.

For the high-density population, biomass of all carp did not drop below 200 kg/ha under any stocking scenario unless the population was extirpated, and the decline in biomass did not occur until stocking of F_{YY} or M_{YY} carp ceased. Although the biomass of the untreated low-density population averaged 108 kg/ha, in some years biomass decreased below 100 kg/ha. However, biomass generally increased when F_{YY} or M_{YY} carp were added to these populations, and similar to the high-density population, biomass only decreased substantially when the population was extirpated and stocking of YY fish ceased.

Rotenone and YY carp stocking.— The probability of extirpating populations under the rotenone treatment was 0.07 for the high-density population and 0.34 for the low-density population when no YY carp were added to the population (Figure 4). If the high-density population underwent a 90% population reduction via a rotenone treatment prior to F_{YY} stocking, the probability of extirpation exceeded 0.50 with a stocking density of at least 200 F_{YY} carp/ha for at least 5 years and exceeded 0.90 with at least 10 years of stocking at 200 F_{YY} carp/ha. If the low-density population underwent a 90% initial reduction in size, the probability of extirpation exceeded 0.88 when at least 50 F_{YY} carp/ha were stocked for at least 5 years or when 25 F_{YY} carp/ha were stocked for at least 10 years.

For M_{YY} stocking, the probability of extirpation following an initial rotenone treatment of the high-density population did not exceed 0.50 for any duration of stocking until stocking density exceeded 600 M_{YY} carp/ha. For the low-density population, probability of extirpation exceeded 0.50 for any duration of stocking for stocking densities at or above 50 M_{YY} carp/ha.

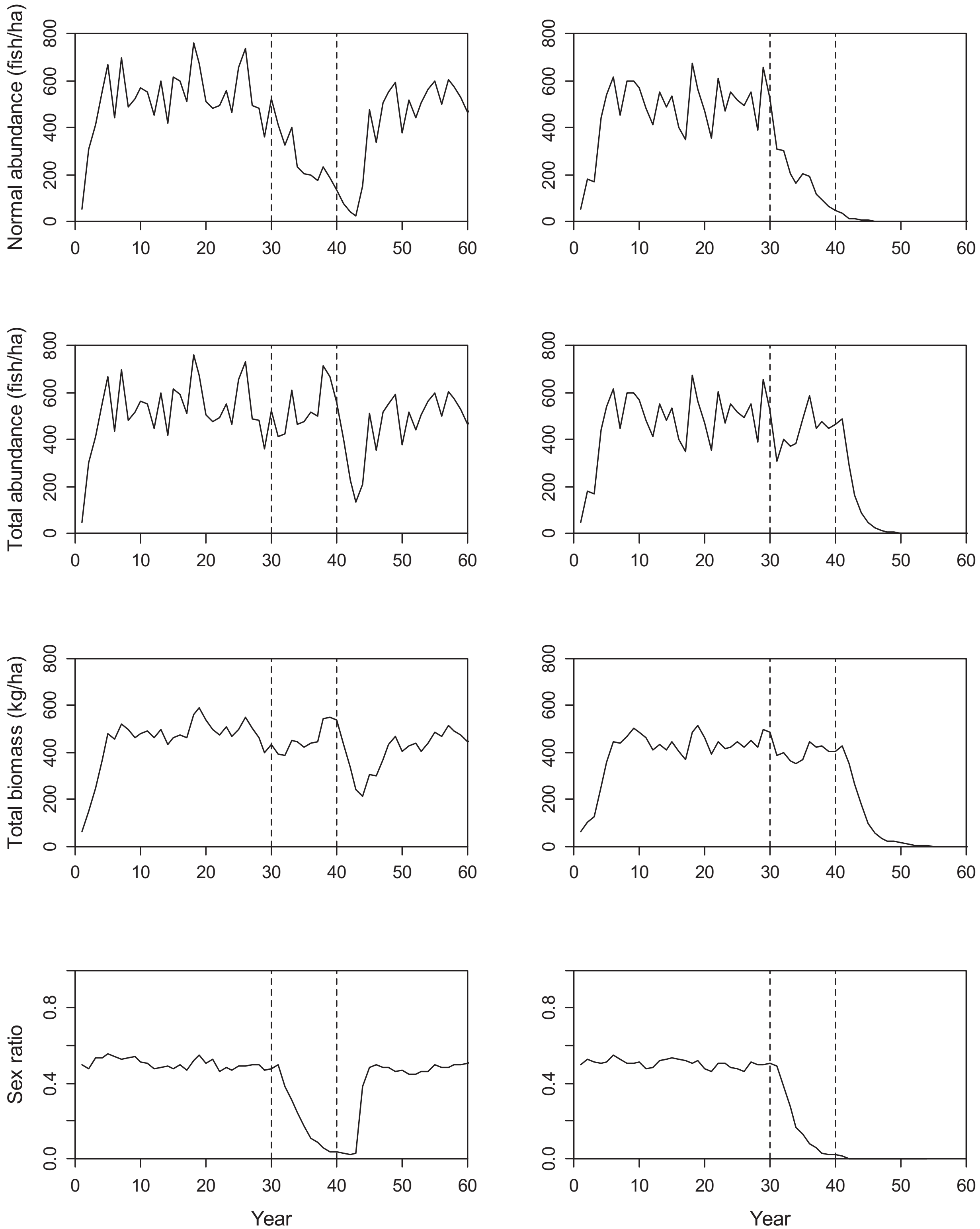

FIGURE 2. Example of simulated population metrics (for a single iteration) for a Common Carp population that persisted (left panels) and a population that was extirpated (right panels). Population metrics that are shown include normal carp abundance (top panels), total abundance (second from top; includes F_{YY} carp), total biomass (second from bottom; includes F_{YY} carp), and sex ratio (proportion female; bottom panels). This example is for the high-density Common Carp population where 100 F_{YY} carp/ha were stocked for 10 years. Dashed vertical lines indicate the beginning and end of the stocking period.

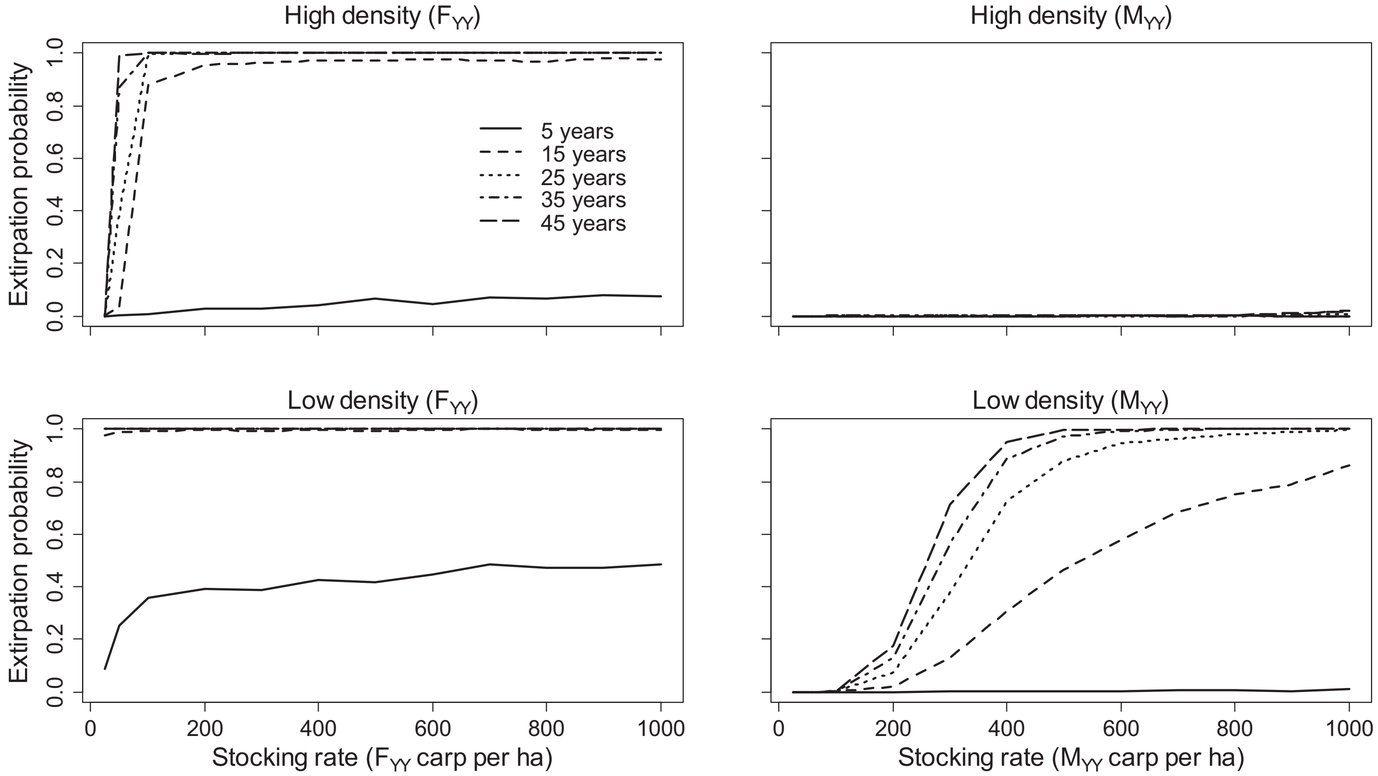

FIGURE 3. Extirpation probability for two population sizes of Common Carp, including a high-density population (top panels) and a low-density population (bottom panels), given F_{YY} (left panels) and M_{YY} (right panels) stocking rates of 25–1,000 Common Carp/ha for 5–45 years.

Biomass of both the low- and high-density populations dropped below 100 kg/ha following the rotenone treatment. However, biomass generally increased above 200 kg/ha for the high-density population and above 100 kg/ha for the low-density population within 10 years of the rotenone treatment—unless the population was extirpated—for all rates of F_{YY} and M_{YY} carp stocking.

Unselective suppression and YY carp stocking.— The extirpation probability was zero for all levels of unselective suppression in the absence of F_{YY} and M_{YY} carp stocking for both the high- and low-density populations. In conjunction with F_{YY} carp stocking, extirpation probabilities exceeded 0.94 for all levels of unselective suppression when at least 100 F_{YY} carp/ha were stocked for at least 15 years (Figure 5). Intermediate levels of extirpation were observed for 5 and 10 years of stocking when unselective suppression levels were less than 75% and stocking densities were less than 400 F_{YY} carp/ha for the high-density population. High probabilities of extirpation were observed with all rates of F_{YY} carp stocking at all unselective suppression levels when they were stocked for more than 5 years for the low-density population. Additionally, when unselective suppression levels were 50% or greater, extirpation probabilities of 0.87 or more were achieved when at least 50 F_{YY} carp/ha were stocked for at least 5 years in the low-density population.

For M_{YY} carp stocking, extirpation probabilities were minimal in conjunction with unselective suppression levels of 10% or less for the high-density population. More than 15 years of stocking at densities of at least 600 M_{YY} carp/ha were required to achieve extirpation probabilities greater than 0.90 for the high-density population for all levels of unselective suppression. At least 25 years of stocking at least 300 M_{YY} carp/ha were required to reach extirpation probabilities greater than 0.80 with unselective suppression levels of 10% and 25% for the low-density population. The duration of stocking decreased to 10 years to achieve an extirpation probability greater than 0.80 when unselective suppression levels increased to 50% and 75%.

For the high-density population, biomass generally decreased below 200 kg/ha when 50% of the population was removed and biomass decreased below the Common Carp target of 100 kg/ha when 75% of the population was removed in the absence of YY carp stocking for all time periods evaluated. All other unselective suppression levels resulted in biomass being above 200 kg/ha for the high-density population in the absence of YY stocking. Additionally, after the suppression effort ended, biomass

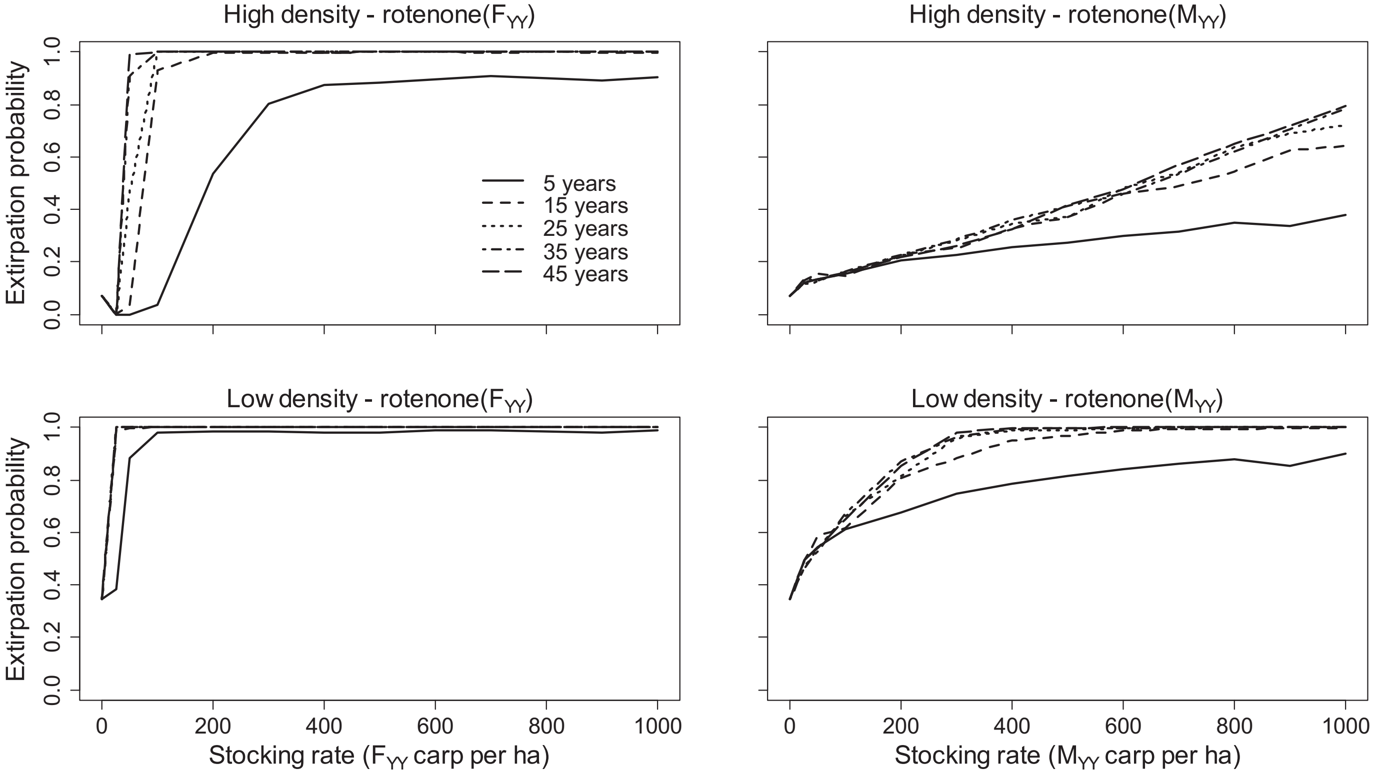

FIGURE 4. Extirpation probability of two population sizes of Common Carp, including a high-density population (top panels) and a low-density population (bottom panels), given F_{YY} (left panels) and M_{YY} (right panels) stocking rates of 25–1,000 Common Carp/ha for 5–45 years after a simulated rotenone treatment that removed 90% of all fish.

increased above 200 kg/ha in all scenarios. Biomass generally was greater than 200 kg/ha for the high-density population when M_{YY} or F_{YY} carp were added to the population at all rates of stocking unless the population was extirpated.

Biomass for the low-density population was less than the 100-kg/ha biomass target for all levels of unselective suppression in the absence of YY carp stocking but returned to baseline levels after suppression ceased. Similar to the high-density population, biomass for the low-density population generally was greater than 100 kg/ha when M_{YY} or F_{YY} carp were added to the population at all rates of stocking unless the population was extirpated.

Selective suppression and YY carp stocking.— Trends in extirpation probability for selective suppression in conjunction with F_{YY} or M_{YY} stocking were very similar to those observed for unselective suppression, with all extirpation probabilities being higher for the selective suppression scenarios (Figure 6). Biomass of the high-density population was generally greater than 200 kg/ha when M_{YY} or F_{YY} carp were added to the population at all rates of stocking and selective suppression unless the population was extirpated. Biomass of the low-density population was less than 100 kg/ha on average at all levels of selective suppression when 50 YY carp/ha or less were added to the population. Biomass was generally greater than 100 kg/ha when more than 50 YY carp/ha were stocked, except in instances where the population was extirpated.

DISCUSSION

Although large reductions in adult Common Carp abundance via sustained manual removal are believed to be a necessary element of successful ecosystem restoration (Weber and Brown 2009), our simulations predicted that some YY male stocking scenarios could eradicate Common Carp populations in reasonable time frames without any need for concurrent manual removal. However, our results suggest that eradication with no concurrent manual removal is feasible only with F_{YY} stocking and highlight that M_{YY} stocking alone would likely be a poor invasive control option for Common Carp. In contrast, far more optimistic extirpation probabilities were obtained in simulations by combining the stocking of F_{YY} or M_{YY} carp with population suppression activities, such as a one-time rotenone treatment or sustained manual removal. Not surprisingly, the use of selective manual removal (i.e.,

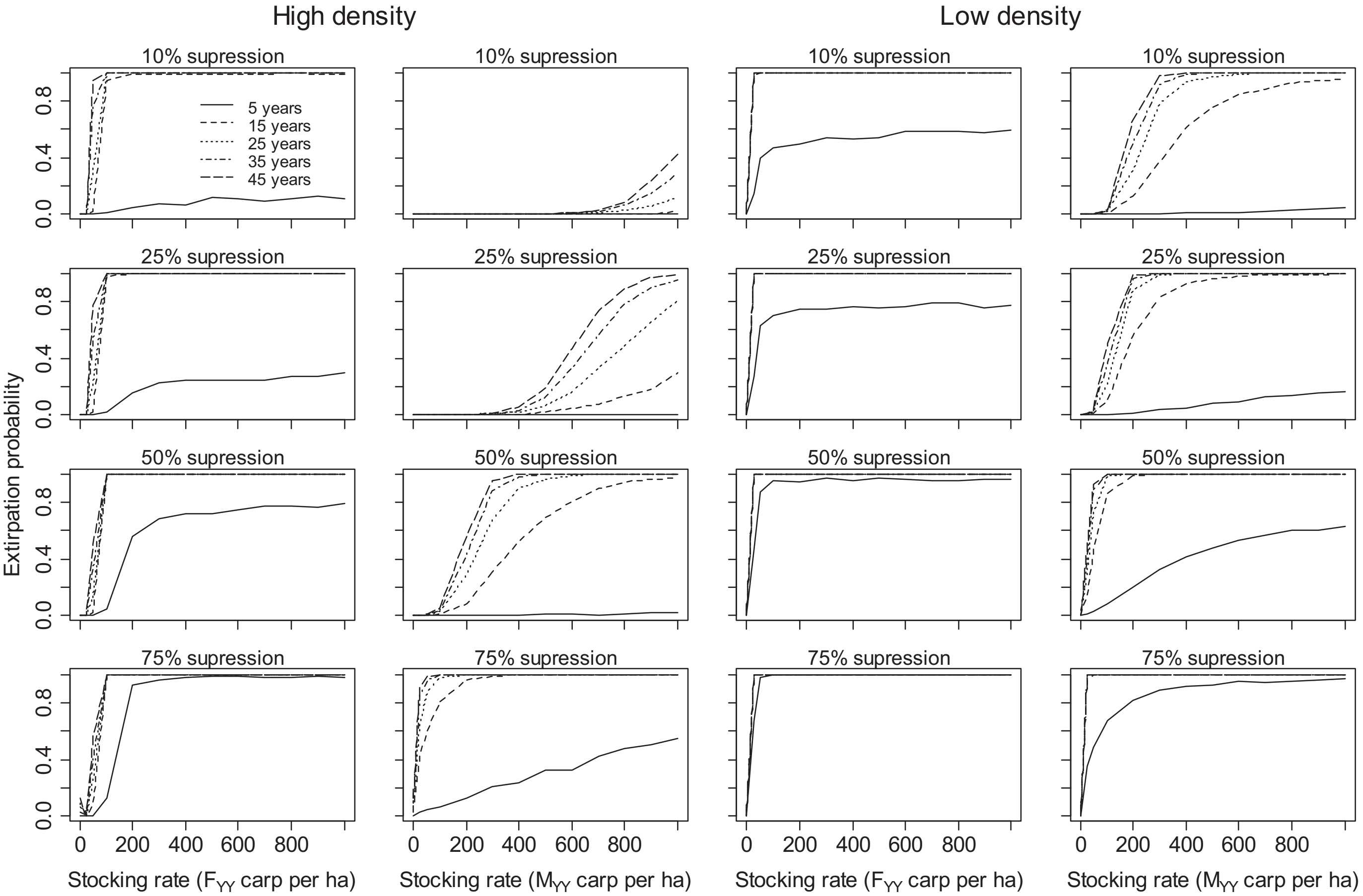

FIGURE 5. Extirpation probability of two population sizes of Common Carp, including a high-density population (left two columns of panels) and a low-density population (right two columns of panels), given F_{YY} and M_{YY} stocking rates of 25–1,000 Common Carp/ha for 5–45 years and simulated annual unselective suppression levels of 10–75% of the population.

avoiding the removal of stocked YY males) increased extirpation probabilities in our virtual populations relative to unselective removal.

Our finding that the stocking of F_{YY} or even M_{YY} carp could theoretically result in sufficiently short population eradication times to be of interest to fisheries managers differs from most prior simulation results for several species of carp using sex-skewing technology. For example, 50–170 years were needed to eradicate Asian carp populations using F_{YY} stocking, depending on stocking rates (Teem and Gutierrez 2010). However, concurrent manual suppression was not evaluated in that study, and it was assumed that only a relatively small number of reproductively competent adult F_{YY} fish were stocked. A suite of IPM control measures, including various manual removal approaches, release of the cyprinid herpesvirus-3, and use of a genetic "daughterless" transgenic construct, was predicted to be successful at reducing Common Carp abundance, but no scenarios extirpated populations or met program biomass reduction targets (Brown and Gilligan 2014). Simulated release of M_{YY} Grass Carp *Ctenopharyngodon idella* also did not effectively suppress virtual populations at stocking rates considered feasible from a management perspective (Erickson et al. 2017). However, Erickson et al. (2017) did not evaluate release of more efficient F_{YY} carp, and they did not combine YY male stocking with manual suppression.

In addition to the simulation studies evaluating sex-skewing technologies noted immediately above, several population modeling studies have evaluated manual removal programs alone for controlling Common Carp populations (Weber et al. 2014; Lechelt and Bajer 2016; Feeken et al. 2019). Although the results varied between studies depending on stocking rates and frequency, taken collectively these studies suggest that suppression levels of 20–50% may be effective at reducing carp abundance to levels below a biomass threshold in some waters to improve water quality, but suppression alone will rarely if ever eradicate carp populations.

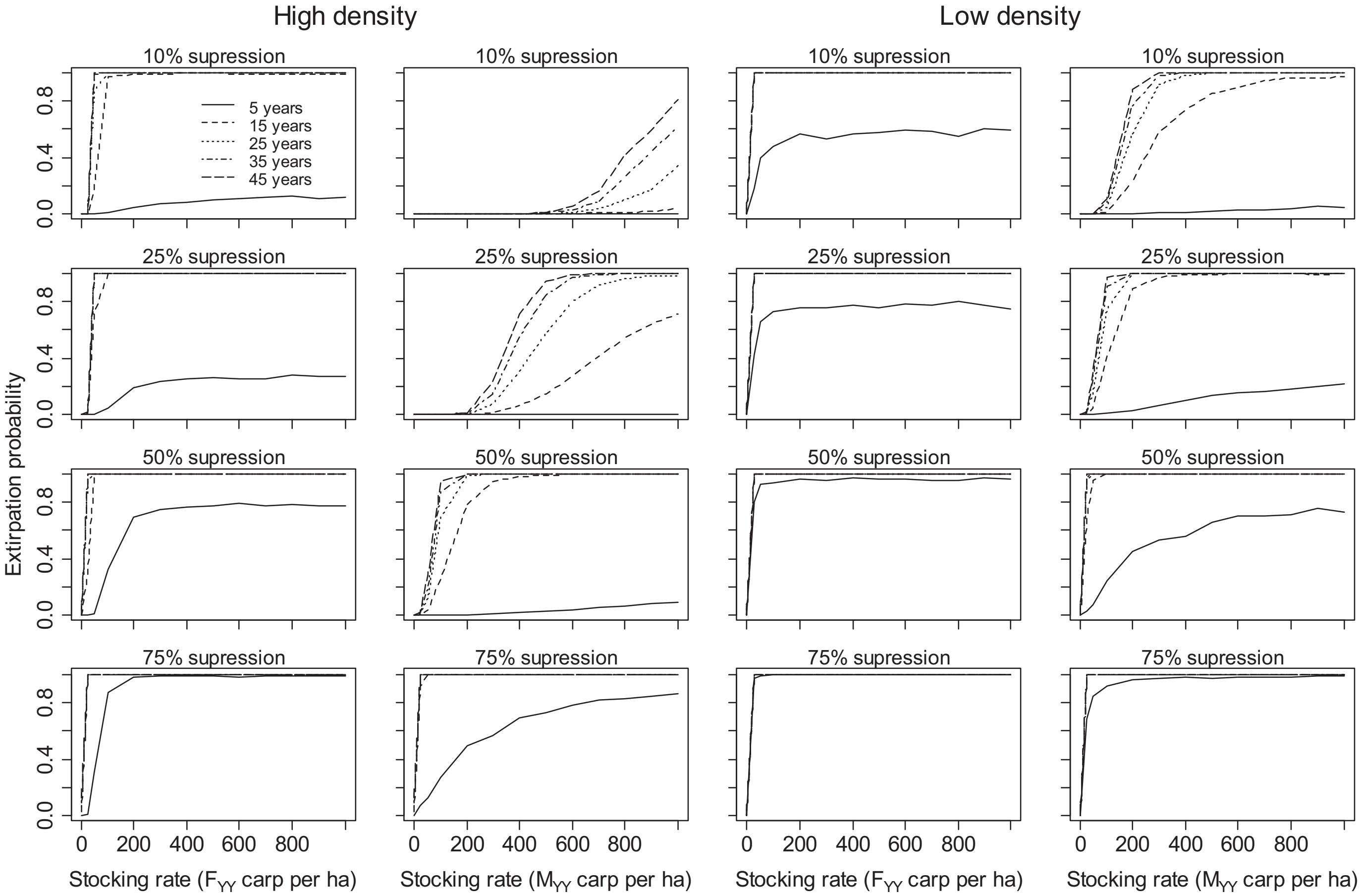

FIGURE 6. Extirpation probability of two population sizes of Common Carp, including a high-density population (left two columns of panels) and a low-density population (right two columns of panels), given F_{YY} and M_{YY} stocking rates of 25–1,000 Common Carp/ha for 5–45 years and simulated annual selective suppression levels of 10–75% of the population.

In contrast, with regard to extirpation, the results of the present study simulations indicate the importance of suppression or exploitation level when stocking YY males, calling for an assessment of what is actually achievable in the field regarding manual carp removal. Few estimates of Common Carp exploitation obtained during actual manual suppression programs are available. In Wisconsin, two to three seine hauls across an entire lake resulted in annual carp exploitation estimates of 19% and 78% in 1954 and 1955, respectively (Neess et al. 1957). More recently, estimates of annual exploitation derived by autumn–winter commercial fishing in three South Dakota lakes were highly variable, but when combined they varied from 9% to 33%, with a mean annual estimate of 19% (Weber et al. 2016). Far higher exploitation estimates of 52, 65–68, and 93% from winter commercial fishing efforts have been reported by authors using specialized commercial angling techniques and radiotelemetry in a process called the “Judas technique” to locate concentrated shoaling winter carp aggregations (Bajer et al. 2011). If sustainable annually, high telemetry or sonar-aided levels of manual carp exploitation at 50–75% combined with F_{YY} stocking could eradicate Common Carp quickly, assuming our simulations are representative of actual populations.

A key question examined in this study was how much more efficacious F_{YY} fish would be in terms of either required stocking numbers or years to extirpation. Of the two possible YY male stocking strategies, F_{YY} stocking functioned far more efficiently in simulations than M_{YY} stocking regardless of the concurrent suppression approaches imposed. Such a finding is not surprising, as from the outset, release of F_{YY} fish was believed ideal because half the progeny of successfully spawning F_{YY} fish in the wild would themselves be M_{YY} carp (Gutierrez and Teem 2006; Teem and Gutierrez 2010). The use of M_{YY} fish theoretically worked in a small subset of scenarios and could prove useful in low-density populations, particularly if the mid-winter, “Judas fish” telemetry approach of Bajer et al. (2011) is used and can consistently facilitate high levels of population suppression. Low-level M_{YY} stocking might also have a prophylactic use in scenarios where complete eradication has occurred but where there is a perceived risk of re-invasion from high-water events or other sources (e.g., Lovas-Kiss et al. 2020).

The above-noted benefit of improved F_{YY} field efficiency may be offset by challenges in their production (Parshad 2011; Teem et al. 2020). A far larger amount of a feminizing hormone will be required to produce large numbers of F_{YY} males for stocking compared to the insignificant amounts used in the production of a broodstock producing M_{YY} males for stocking, as noted by Schill et al. (2016). Large-scale F_{YY} production will thus likely result in increased oversight by the U.S. Food and Drug Administration, though the issue should not prove insurmountable because the tissue retention times of estrogens in fish exposed to exogenous hormones for sex control are quite short (Johnstone et al. 1978; Piferrer and Donaldson 1994) and release of a feminizing hormone into the environment can be controlled by charcoal filtration (Specker and Chandlee 2003; Silva et al. 2012). Nonetheless, the more efficient performance of feminized F_{YY} carp in our simulations will complicate the process of producing large numbers of YY males for release as a more effective eradication tool.

One important disadvantage of an IPM program involving manual or piscicide suppression and YY male stocking relates to the timing of associated water quality improvements. As noted previously, many current manual removal programs contain carp suppression targets, typically 50 or 100 kg/ha, the attainment of which is believed to improve water quality and improve ecosystem function (Brown and Gilligan 2014; Lechelt and Bajer 2016; Pearson et al. 2019). Unfortunately, the stocking of large numbers of YY male fish in our simulations did not allow such targets to be attained until stocking ceased. Similar results were observed in IPM stocking of the daughterless construct (Brown and Gilligan 2014). There appears to be a tradeoff between the greater likelihood of complete eradication via use of YY male fish and water quality improvements along the way.

Despite the promising results of virtual F_{YY} stocking in the present simulation study, the requisite technology for their production is not yet complete because male carp have heretofore proven resistant to feminization (Komen et al. 1989; Teem and Gutierrez 2010). However, a recent study yielded a feminization rate of 58% for a single sample of 48 male fish (Jiang et al. 2018) and an accurate sex marker has recently been developed for several U.S. Common Carp populations (Mathew Campbell, Idaho Department of Fish and Game, unpublished data). Nonetheless, additional feminization trials are necessary for the production of a YY male broodstock capable of producing large numbers of F_{YY} or M_{YY} fish for release into wild carp populations. We would note, however, that even if 100% feminization proves elusive, stocking F_{YY} fish that are partly comprised of M_{YY} fish would only slow the eradication process, not prevent it.

It would seem useful to put several of our simulation scenarios into perspective relative to both past virtual and actual wild Common Carp populations. Our virtual high-density population at initialization simulated an unmanaged carp population of 508 fish/ha or 467 kg/ha, similar to the values of 400 fish/ha and 500 kg/ha for the recent virtual initialized population of Lechelt and Bajer (2016). Our virtual low-density population at initialization simulated an unmanaged carp population of 150 fish/ha and 198 kg/ha, similar to actual carp abundance values of 115 fish/ha and 234 kg/ha reported for 10 relatively small Midwestern U.S. lakes considered to be low-density (Bajer and Sorensen 2012). Assuming that our simulation results are scalable to waters of various sizes, managers can approximate numbers of F_{YY} and M_{YY} fish that would theoretically need to be reared and stocked annually to eradicate individual carp populations with various degrees of likelihood. For example, treating a low-density carp population in a 50-ha lake with rotenone (achieving a one-time 90% carp suppression rate) and subsequently stocking it at 100 F_{YY} carp/ha would require 5,000 stocked fish annually, with a predicted extirpation probability of 0.98 within 5 years. Conversely, stocking a 400-ha lake containing a high-density carp population at a stocking rate of 100 F_{YY} carp/ha while selectively exploiting at 75% would require 40,000 stocked fish annually, yielding a predicted extirpation probability of 0.80 within 5 years. While both of these scenarios may prove feasible both from a fisheries management time frame and from a hatchery resource allocation perspective, in general the treatment of smaller waters with lower density carp populations will inherently be more practical for implementing a YY male stocking program. Larger waters with higher density carp populations may require too many field suppression or hatchery production resources to be considered feasible.

There is a number of assumptions inherent in our simulations that comprise study limitations of varying import. The biggest limitation of our approach is that, like van Poorten et al. (2019), we assumed a closed population, which may not exist in a given situation, particularly in complex Midwestern waters containing Common Carp (e.g., Bajer and Sorensen 2010). We further assumed that stocked F_{YY} and M_{YY} fish experienced mortality similar to that of wild fish after stocking (Gutierrez and Teem 2006; Teem and Gutierrez 2010; Parshad 2011) and also that reproductive fitness of stocked YY male and wild fish were equal. Direct data for Common Carp do not exist to permit evaluation of these assumptions, though failure to meet either would result in over- or under-optimistic extirpation predictions. Kennedy et al. (2018) reported that M_{YY} Brook Trout *Salvelinus fontinalis* were slightly less fit overall relative to wild fish, but these results were for a species that generally does not survive well when stocked in streams. Conversely, YY male carp stocked in lentic settings at sizes larger than most sight-feeding predators consume may fare better than small, wild age-0 carp. In addition, fish stocked in waters where wild populations are strongly suppressed have been reported to have over twofold survival increases (Schill et al. 2017). In terms of initial reproduction potential, gonads of sex-reversed fish can function well. For example, M_{YY} fish had better spermatic quality than normal XY males in Nile Tilapia *Oreochromis niloticus* (Salirrosas et al. 2017), and F_{YY} fish had slightly higher fecundities than standard XX females in a YY male Brook Trout broodstock (Schill et al. 2016). We further assumed that both stocked and wild carp randomly selected mates in proportion to their relative abundance (Gutierrez and Teem 2006; Teem and Gutierrez 2010). It is currently unknown whether a wild fish would be able to discriminate between wild and YY males (Erickson et al. 2017). Additionally, we assumed that all F_{YY} carp in the population mated each year and that fish of all sizes were equally vulnerable to the rotenone treatment. Finally, like most other YY male studies (e.g., Lyu et al. 2019), we used a single natural mortality rate in our simulations; the mortality rate was from a high-density Idaho Common Carp population that was also somewhat short-lived (Figure 1). Longer life span and longer generation times would likely result in less optimistic extirpation predictions, though such populations would likely be more vulnerable to exploitation and recruitment overfishing. In addition, we assumed that age-0 YY male carp did not undergo the same density-dependent mortality process as naturally produced carp but instead shared the same annual mortality parameter as the remaining age-classes. This assumption may be met in practice if age-0 fish are stocked after density-dependent processes take place or if they are stocked at a larger size to gain a competitive advantage over their natural cohorts. However, if this assumption is not met in practice, the simulation results related to the efficacy of YY male stocking in the current study are likely optimistic. Our simulations comprised the first examination of YY male potential for Common Carp eradication, and additional tests of the above assumptions are warranted in the future.

CONCLUSIONS

Many of the more effective invasive species suppression approaches to date involve what has been termed a “brute force or scorched earth approach,” but there is no reason why research cannot devise a better mousetrap (Simberloff et al. 2005). Brute force methods employed in control of Common Carp have historically included seines, gill nets, piscicides, and rarely, electrofishing. One could argue that bubble curtains, pheromones, the Williams’ cage, use of radiotelemetry to find winter aggregations, piscicide-laced baits, and a suite of recruitment-related approaches for reducing access to spawning and early rearing habitat all comprise research efforts to devise a better mousetrap, with varying levels of success. However, with the exception of rotenone use, invasive Common Carp have rarely been completely and permanently extirpated from waters worldwide, and as has been noted, there is considerable room for improvement in invasive fish control efforts (Meronek et al. 1996).

Based on our study results, we suggest that the stocking of YY male Common Carp constitutes a novel method worthy of further consideration if they can be developed. Though our results suggest that F_{YY} stocking by itself could completely eradicate Common Carp populations, the simulations clearly show that their stocking plus concurrent employment of other suppression approaches in a multi-pronged IPM program will more rapidly reduce overall carp densities and increase the likelihood of complete population collapse. The large difference in relative success between M_{YY} and F_{YY} stocking appears to be related to two factors. The first and foremost is the fact that on average, 50% of F_{YY} progeny will themselves be M_{YY}, further speeding the extirpation process. A second factor, the high fecundity of female carp, also appears to play a role. In essence, the latter approach involves fighting fire with fire. Additional simulations are needed to flesh out important remaining issues not undertaken in this first simulation study, which was largely designed to evaluate the relative efficacy of F_{YY} versus M_{YY} with and without additional suppression approaches.

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Appendix 1 Sensitivity analysis

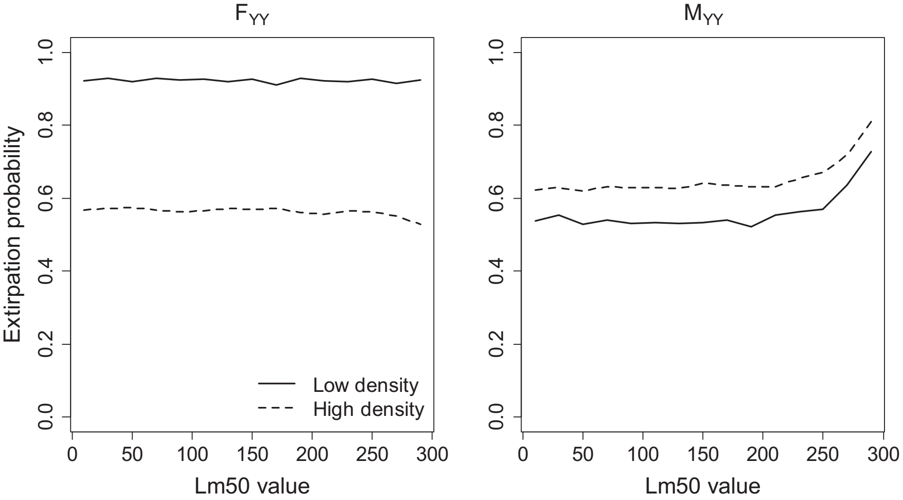

FIGURE A.1. Sensitivity analysis to evaluate the effect of the length-at-maturity parameter (Lm50, mm) on the probability of extirpation for two Common Carp population densities. For the F_{YY} analysis, 200 F_{YY} carp were stocked for 10 years into both the low- and high-density populations. For the M_{YY} analysis, 300 M_{YY} carp were stocked for 35 years into the low-density population and 1,800 M_{YY} carp were stocked into the high-density population.