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A Theoretical Strategy for Eradication of Asian Carps Using a Trojan Y Chromosome to Shift the Sex Ratio of the Population

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Abstract.—The directed extinction of an exotic fish population is proposed using a genetic approach to drastically reduce the ratio of females to males within the population. In the proposed strategy, sex-reversed female fish containing two Y chromosomes (Fyy) are introduced into a normal fish population. The frequencies of each of the four expected genotypes of fish in the simulated population (Fxx, Fyy, Mxy, and Myy) were modeled with a set of coupled ordinary differential equations. The equations take into account birth rate, death rate, and a fixed carrying capacity of the system. Using computer-generated simulations, it was determined that the continuous introduction of a relatively small proportion of Fyy females to the normal population leads to extinction of the exotic fish over time. The proposed eradication strategy is relevant to fish species with an XY sex-determination system and that tolerate a YY genotype. Published literature suggests that Asian carps are likely to fulfill these criteria. However, technical barriers associated with sex reversal in Asian carps presently exist and must be overcome before implementation of a YY eradication strategy for Asian carps can be considered in practice. An idealized theoretical model for the eradication of Asian carps is thus presented.

Introduction

Due to their widespread distribution, Asian carps represent a particularly challenging problem with respect to eradication strategies. In most cases, Asian carps are found in large complex water systems, making conventional chemical means for the eradication of fish unfeasible. Grass carp *Ctenopharyngodon idella* are present through much of the United States (Fuller et al. 1999). Bighead carp *Hypophthalmichthys nobilis* and silver carp *H. molitrix* are established and distributed throughout the Mississippi basin (Conover et al. 2007). Recently, black carp *Mylopharyngodon piceus* were found in several water systems in the Midwest (Chick et al. 2003). Genetic approaches may offer an alternative means to eradicate carps from the affected water systems. A genetic approach to eradication that limits carp reproduction has the additional advantage of selectively targeting nonnative carps and leaving the native fish unharmed.

Genetic strategies for population control have previously been limited to efforts that decrease productive matings as a result

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of releasing sterile males into the population. For example, the release of large numbers of sterile male Mediterranean fruit flies *Ceratitis capitata* in Florida was used successfully to reduce the probability of productive matings between fertile males and females (Knipling 1955). This approach was also used to reduce the frequency of productive matings between sea lampreys *Petromyzon marinus* in the Great Lakes (Twohey et al. 2003). One significant limitation of this approach is the requirement to introduce an overwhelming number of sterile males in order to compete with fertile males in the population. If insufficient numbers of sterile males are released, normal matings may occur in sufficient numbers to maintain the population. This problem may be particularly relevant to the use of a sterile release strategy for bighead and grass carps as it is known that females of these species have multiple mating partners (Jennings 1988; Opuszynski and Shireman 1995).

Hamilton (1967) proposed that extraordinary sex ratios could lead to local extinction; thus, an alternative approach to eradication could involve shifting the sex ratio of the population over time, such that one sex is eventually eliminated. In one novel genetic approach to the eradication of exotic fish, a genetic "Trojan fish" is added to the target population, shifting the sex ratio over time and ultimately resulting in the elimination of females (Gutierrez and Teem 2006). The strategy involves the addition of female fish bearing multiple Y chromosomes (Fyy) at a constant rate to a target population containing normal females (Fxx) and normal males (Mxy). Matings between the introduced Fyy fish and the resident Mxy fish generate a disproportionate number of male fish in the progeny of successive generations. Over time, the higher incidence of males produced in the progeny shift the ratio of females : males downward in the population. Ultimately, normal females decline to zero, causing the extinction of the population.

This "YY" eradication strategy requires that the target fish has an XY sex-determination system, and that viable female fish with a YY genotype can be produced through standard aquaculture techniques. Based upon sex ratios of meiotic and mitotic gynogenetic progeny, an XY sex-determination system has been reported for silver carp (Mirza and Shelton 1988; Devlin and Nagahama 2002) and grass carp (Stanley 1976; Shelton 1986). Similar genetic studies on the sex-determination system of bighead carp are lacking; however, the observation that silver carp and bighead carp produce fertile hybrids suggests that these species are genetically closely related and thus likely to share an XY sex-determination system (Chapman and Deters 2010, this volume). This notion is further supported by the observation that grass and bighead carps also produce viable hybrids (Bettoli et al. 1985). For the more distantly related common carp *Cyprinus carpio* L., androgenetic reproduction techniques have also indicated the presence of an XY sex-determination system (Bongers et al. 1999). Sex determination in black carp has not been investigated extensively, although viable hybrids have been reported resulting from crosses of common carp and black carp (Makeyeva and Verigin 1993). Taken together, these results suggest that Asian carps utilize an XY sex-determination system.

In addition to an XY sex-determination system, the YY eradication strategy additionally requires that viable female fish of the target species can be produced with a YY genotype through standard aquaculture techniques. For Nile tilapia *Oreochromis niloticus*, YY males can be produced by first reversing the sex of genotypic males using estrogen analogs such as DES (producing a phenotypic females with both an X and Y chromosome, Fxy) and subsequent breeding of these Fxy fish to normal males (Mair et al. 1997). Additional means of producing Nile tilapia YY males through gynogenesis have also been described (Varadaraj and Pandian 1989). However, difficulties are encountered when these same methods are applied to common carp (Bongers et al. 1999; Komen et al. 1992), silver carp (Mirza and Shelton 1988), and grass carp (Shelton 1986; Opuszynski and Shireman 1995). Viable and fertile YY males (*M*yy) have been produced in common carp using androgenesis (Bongers et al. 1999) rather than gynogenesis; however, androgenesis is technically difficult and has not yet been successfully used for producing YY Asian carps. Theoretically, it should be possible to produce female YY carps (Fyy) through estrogen induced sex reversal of Myy juveniles; however, in practice the feminization of carps has proven to be inefficient (see Discussion). Uncertainty thus currently exists regarding the technical limitations of producing of Fyy Asian carps. However, for the purpose of considering the theoretical possibilities of eradicating Asian carps through a YY eradication strategy, we will assume for the present that these technical barriers can be overcome.

Methods

Population dynamics can be modeled with differential equations if the population is large enough (i.e., if the influence of single individual is negligible). There are two types of differential equations: (1) those that consider only variation in time with respect to a set of parameters (i.e., ordinary differential equations [ODEs]), and (2) those that consider temporal and spatial variation in the same model (i.e., partial differential equations [PDEs]). The choice of the type of model depends upon the species being modeled and the size of the spatial domain. For example, fish (not necessarily Asian carps) introduced into a 1-acre (0.4 ha) pond could be considered instantly evenly distributed throughout space, making spatial variation negligible; in this case, a system of ODEs would be appropriate. If we consider a much larger target area, such as the river systems of the Mississippi basin, the spatial component could not be overlooked because the population front moves relatively slowly through the system over time, making necessary a system of PDEs. However, we are more concerned with the qualitative behavior of the system rather than the exact numerical solution; thus, an ODE system is valid.

It was reported by Gutierrez and Teem (2006) that the population dynamics of a fish system involving Fxx, Fyy, Mxy, and Myy individuals in a spatial-independent setting could be modeled with a system of ODEs. A spatial model would elaborate on the ODE system by introducing a diffusion term. This would account for spatial variation and introduce additional complexity with respect to the ODE system (i.e., we would end up with a PDE model). The solution of this one-dimensional, Dirichlet-type, PDE model using, for instance, finite differences, would be equivalent to the solution of many discrete ODE models with initial conditions given by the spatial constraints (Quarteroni et al. 2000); furthermore, each ODE system, in this particular case, will behave qualitatively as the ODE system proposed by Gutierrez and Teem (2006), if constant initial conditions are assumed. When initial conditions are known precisely (i.e., when the population density of Asian carps can be estimated along a riverine system) the spatial model should be used to predict the outcome of a real scenario. For the theoretical purposes of this paper, we will use ODE equations similar to those proposed previously.

A coefficient for death (D) was associated with each of the four fish genotypes (Fxx, Mxy, Myy, and Fyy) and acts to decrease the numbers of fish in the population. In contrast, a birth coefficient (B) was associated with each equation representing Fxx, Mxy, and Myy, increasing the numbers of these genotypes as a result of matings. In this paper, we have introduced a new parameter, a constant that represents the proportion of fish entering the reproductive pool, which we have called α. Since the population size is limited by the carrying capacity, the number of individuals added to the system must be in equilibrium with the number of individuals that leave the reproductive pool. Thus, the birth coefficient takes the following value:

$$B = \alpha D. \tag{1}$$

The parameter α used in equation (1) indicates that the number of individuals that arise and develop to sexual maturity is equal or less than the number of births. One reason for representing birth rate in terms of death rate is that all four genotypes are assumed to be affected equally by the death coefficient; however, only three of the genotypes (Fxx, Mxy, and Myy) can be obtained by reproduction in the system, and therefore there is a relationship between the birth and the death rate. For the Fyy fish, which does not arise by reproduction, the birth rate is artificially controlled and thus is independent from the death rate. Another reason for representing the birth coefficient in terms of the death coefficient is that the system is highly sensitive to the death coefficient and has very little sensitivity to the birth coefficient. It should be noted that the coefficient D will also be affected by harvesting, an intervention that could be applied as a means of augmenting the eradication strategy. However, for our purposes, we will not address the specific effects of harvesting independent from its contribution to D. The coefficient B can be replaced in the original formulas to yield the following system of ODEs:

$$\frac{d}{dt}\mathrm{Fxx} = 0.5\mathrm{FxxMxy}\alpha DL - D\mathrm{Fxx}, \tag{2}$$

$$\frac{d}{dt}\mathrm{Myy} = \left(0.5\mathrm{FyyMxy} + \mathrm{FyyMyy}\right)\alpha DL - D\mathrm{Myy}, \tag{3}$$

$$\frac{d}{dt}\mathrm{Mxy} = \begin{pmatrix} 0.5\mathrm{FxxMxy} + 0.5\mathrm{FyyMxy} \\ + \mathrm{FxxMyy} \end{pmatrix}\alpha DL - D\mathrm{Mxy}, \tag{4}$$

$$\frac{d}{dt}\mathrm{Fyy} = \mu - D\mathrm{Fyy}, \tag{5}$$

$$L = \left(1 - \frac{\mathrm{Fxx} + \mathrm{Fyy} + \mathrm{Mxy} + \mathrm{Myy}}{K}\right), \tag{6}$$

where

D = dimensionless proportionality constant that accounts for the death of individuals that reproduce within the population.

α = dimensionless proportionality constant that accounts for the differences between birth and death rates.

K = carrying capacity of the ecosystem.

μ = constant influx of Fyy.

Each ODE represents the frequency of one of the four types of fish in the population. The frequency of Fxx, Mxy, and Myy fish in the progeny is determined by the relative frequency of the parent fish of the four possible mating pairs (Gutierrez and Teem 2006). Because the Fyy fish is an introduced fish (and not generated by matings within the system), the equation describing the frequency of Fyy fish is lacking B, but instead contains a coefficient μ. The coefficient μ represents the rate at which Fyy fish are added to the system. The value of μ is analogous to a stocking rate, and represents the one component of the system that can be manipulated experimentally. A logistic term (L) acts as an attractor with respect to the carrying capacity of the system (i.e., if the total population, given by Fxx + Fyy + Mxy + Myy, is below the carrying capacity, the logistic term is positive and thus the population grows; otherwise, the logistic term becomes negative, producing population decay). The logistic model was chosen because of its simplicity and because of the lack of experimental data. It is assumed that the population increases to the carrying capacity of the system, at which point it remains constant. Even though the number of one specific genotype might decrease, other genotypes simultaneously increase, such that the total population remains close to the carrying capacity.

The range of parameters was chosen based on purely theoretical grounds. The value of D was chosen in the range [0.1, 0.3], which means that at any point in time, between 10% and 30% of the reproductive adult population is dying. The value of α was chosen in the range [0.1, 100], with the preferred value being $\alpha = 1$, which means that the number of individuals that are introduced into the reproductive pool is the same as the number being removed from it. The large range for α in the model demonstrates that the behavior of the system has little sensitivity to it.

In the model, initial conditions were set such that the starting population contained 100 Fxx and 100 Mxy fish, and the carrying capacity was set to a maximum of 300 fish. Birth (B) and death (D) coefficients were set within a fixed range, and the starting number of Fyy fish was set to zero. The numbers are arbitrary; the number of 100 could represent 100 thousand, 100 million, and so forth. The initial conditions have little effect in the long-term outcome because the population is kept within the limits of the carrying capacity set by the attraction of the logistic term.

Several assumptions were made regarding the behavior of the YY fish (Fyy and Myy) in the model. For modeling purposes both Fyy and Myy fish are assumed to mate and persist in the population with equal efficiency to wildtype (see Discussion). The YY genotype is thus assumed to confer no selective advantage or disadvantage to fish within the population.

The dynamical system described was calculated with nonstiff predictor-corrector Adams method, with dynamic monitoring of whether stiff backward differentiation formula (BDF) method should be used in subsequent steps. Results were validated using fourth-order Runge-Kutta with adaptive steps (XPP, tolerance = 1E-10, minimum step = 1E-10, maximum step = 1.) A finite-difference model with a forward-time, center-space stencil was used to validate the spatial components, using a diffusion coefficient in the range [0.01, 0.001]

Results

The types of progeny expected from the mating of fish with an XY sex-determination system is shown in Table 1 (Punett square A). Females (Fxx) produce only gametes containing X chromosomes, whereas males produce gametes containing either an X or a Y chromosome. A 1:1 progeny ratio of females: males results from the equal contribution of X and Y containing sperm to the X-containing gametes of the female, and this ratio reflects the proportion of females:males in the general population as well. The initial sex ratio of a population of Asian carps in the wild can thus be represented by Table 1A (Fxx × Mxy). If female fish bearing multiple Y chromosomes are added to the initial population, the ratio of females:males in the progeny (and consequently the Fxx population) is decreased. This occurs because matings between the Fyy female with normal males (Table 1B) generate exclusively male progeny

Table 1. The four mating pairs resulting in the population after the addition of Fyy fish. In the initial native population, only XX females and XY males are present (Punett square A, dotted-line box). This population produces only XX females and XY males in a 1:1 ratio. If YY females are added (Fyy), these introduced fish are able to mate with XY males (Punett square B) to produce all male progeny consisting of half XY males and half YY males (bold). The new YY males in the population can now mate with normal females (C) or YY females (D), in each case producing only male progeny. Thus, as a result of adding the Fyy fish, the population consists of four different kinds of fish that collectively favor the production of male progeny. If each fish were present in equal numbers, males are favored 7 to 1 over females. Since the numbers of YY males should increase over time, it is hypothesized that the number of female progeny will decline over time, eventually to zero.

A		Mxy	
		X	Y
Fxx	X	XX	XY
	X	XX	XY

C		Myy	
		Y	Y
Fxx	X	XY	XY
	X	XY	XY

B		Mxy	
		X	Y
Fyy	Y	XY	YY
	Y	XY	YY

D		Myy	
		Y	Y
Fyy	Y	YY	YY
	Y	YY	YY

composed of 50% normal males (Mxy) and 50% “supermales” (Myy). In subsequent generations, the Myy males will produce only male progeny (Table 1C, D) in matings with either Fxx, or Fyy females, further contributing to a decrease in the ratio of females:males within the population. The addition of Fyy fish to the initial population thus results in four types of fish (Fxx, Fyy, Mxy, and Myy) in the population and four types of possible mating pairs (Table 1A: Fxx × Mxy, B: Fxx × Myy, C: Fyy × Mxy, and D: Fyy × Myy). Collectively, these four different matings produce three types of progeny fish (Fxx, Mxy, and Myy) in the ratio of 2:8:6. The relative proportion of each fish in the population will determine the actual numbers of each type of fish produced at each generation. Thus, the continued production of Myy males at each generation will be expected to drive the number of females down accordingly over time.

The decline of Fxx females as the result of addition of the Fyy fish within the target population is shown in Figure 1. In this example, the value of μ was set to 5.0 (representing a continuous annual influx of five Fyy fish to population with a carrying capacity limit of 300 and $\alpha = 1$). The decline of normal females (Fxx) is continuous through the time course of the experiment and reaches zero at approximately $t = 170$. The number of Mxy males similarly declines after a short lag. In contrast, Myy fish increase in abundance throughout the time course. The number of introduced Fyy fish initially increase and then reach a stable plateau that is dependent upon the value of μ. Although the Fxx decrease to zero at $t = 170$, termination of further Fyy additions must cease once normal females Fxx are eliminated in order for the extinction of the population to occur.

Shown in Figure 2 are the consequences of changing the value of μ in the system. If μ is reduced to 1 (below the minimum value of 3.85 required for extinction), the number of Fxx does not continuously decline, but instead

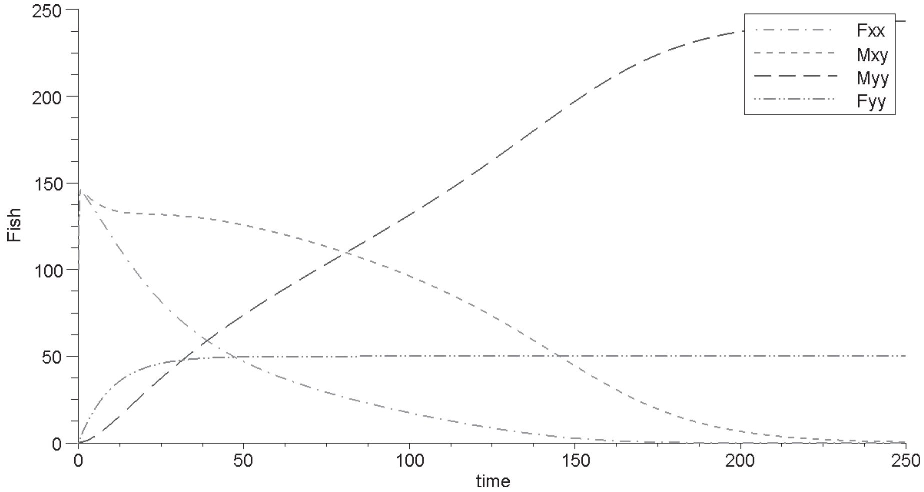

Figure 1. Graphic modeling of the target population containing Fxx, Fyy, Mxy, and Myy fish. Calculations were made with the following parameters: $D = 0.1$; $\alpha = 1$; $K = 300$; $\mu = 4$. Units of time correspond to years, the time associated with the mating cycle of Asian carps.

stabilizes at a value slightly lower than the initial starting value of 100. In contrast, increasing the parameter μ to 10 results in an accelerated decline of females, with extinction occurring at $t = 80$ as compared to $t = 170$ ($\mu = 5$). It is thus apparent that extinction of the Fxx females in the population can be achieved in a time span of less than $t = 80$ if the number of Fyy females added to the population can be increased to 3.3% of the total target population. A value of $\mu = 30$, corresponding a stocking rate of Fyy females equal to 10% of the total target population, reduces the time frame even further ($t = 50$).

In the mathematical model system, the kinetics of the change in population is dependent upon several factors. The value of μ is par-

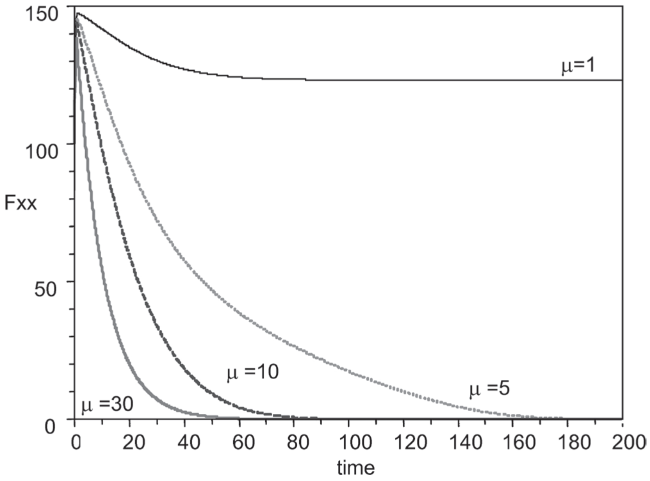

Figure 2. Graphic modeling of the target population containing Fxx fish with different values of μ. Calculations were made with the following parameters: $D = 0.1$; $\alpha = 1$; $K = 300$. The value of μ was set to 1, 4, 10, and 30. As the value of μ is increased, the time needed to achieve eradication is reduced.

ticularly important as this represents a value that can be increased as a means to decrease the time required for extinction. For example, for the model population under consideration, maintained at 300 fish due to the limit set by the carrying capacity and $\alpha = 1$, this corresponds to a stocking rate of 3.85 Fyy fish added continuously over time at annual intervals. The Trojan Fyy fish must therefore be added continuously in amounts that correspond to at least 1.28% of the total target population if extinction is to occur. The time frame for extinction is on the order of decades when the rate of Fyy introduction is kept close to the minimal value of 3.85.

The results of a bifurcation analysis testing a range of values for B, D, and α with respect to the parameter μ suggest that extinction of the initial population will occur over time, provided the value of μ (the rate of addition of Fyy fish) reaches a critical value given by the point of inflection of each saddle-node bifurcation (data not shown). These data indicate that for a range of values of α, there is a corresponding value of μ, which will assure extinction of the population.

Discussion

Asian carps are likely to employ a XY sex-determination system; thus, a theoretical YY eradication approach may be considered for their eradication in a riverine system. As shown in the model studied, eradication can be achieved if the value of μ (the rate at which Fyy fish are added to the system) is set at a sufficiently high value above the minimum determined by the bifurcation analysis (Gutierrez and Teem 2006). For the model presented, the minimal value of μ corresponds to 1.07% of the total carp population, added at a constant rate throughout the time course of eradication.

The parameters α and μ drive the dynamics of the system. The values of these parameters used in the numerical experiments are hypothetical; it is important to emphasize that these parameters must be determined experimentally. They are expected to be different for each species and even to have variation for the same species depending upon local conditions. A bifurcation analysis done for the parameter α reveals that the required stocking rate of Fyy varies very little for a large range of different birth and death rates. The parameter α corresponds to a natural condition and thus cannot be controlled in the wild; the parameter μ, on the contrary, is the only parameter that can be controlled.

The model assumes that all Fyy fish added to the system are reproductively competent adults; however, it would be more practical from a fisheries perspective to produce and stock juveniles to the target system. Since the model does not address the mortality associated Fyy juvenile fish prior to their maturation, stocking rates would require adjustment to compensate for this factor. Other practical considerations limiting the production of Fyy fish may be associated with specific biological attributes of each Asian carp species. For example, hormone-induced sex reversal of fish is most easily accomplished by feeding juveniles with feed containing hormone, but this method was found to be inefficient for use with grass carp (Shelton 1986). Efficient sex reversal in grass carp was only achieved with hormone-containing silastic implants, a more labor-intensive procedure that may not be amenable to high levels of production. If sex reversal of Asian carps are not amenable to conventional approaches, this will represent a technological barrier that must be addressed before the large-scale production of Fyy Asian carps can be considered.

Given the parameters used for the model, the results suggest that many decades of intervention will be required before extinction of the target population is attained. The units of time indicated in Figures 1 and 2 correspond to the interval between mating periods, which is approximately 1 year for Asian carps (Abdusamadov 1986; Conover et al. 2007). New fish entering the system additionally require time for maturation, but represent a small number of the total population; thus, the effect of maturation has little impact on the outcome of the system if the population is large. For a time scale in which one unit equals to 1 year, the time frame required for extinction resulting from addition of the minimum amount of Fyy (μ = 3.2) is approximately 170 years. However, this time frame can be shortened by increasing the influx of Fyy fish into the system; for instance, with μ = 30, the time required for extinction is about 40 years.

Although Asian carps appear to have an XY sex-determination system, it is unknown whether autosomal factors are additionally involved in sex determination. As observed with Nile tilapia (Lee et al. 2003), sex determination in carps may be subject to the effects of additional autosomal genes. It is not presently known how secondary sex-determination genes may affect the Trojan YY eradication system. Additional research to assess the effects of autosomal sex-determination genes in Asian carps will be required in order to determine whether minor sex-determination factors will play a role in affecting the kinetics of the decline of Fxx females.

A "daughterless carp" strategy has been suggested as an alternative genetic approach to eradicate exotic carps by reducing the number of females in the population (Thresher et al. 2002). In this strategy, each chromosome of a Trojan fish is first engineered to express an inhibitor of aromatase, an enzyme required for female hormone production. The resulting transgenic fish is then introduced into the target population over the course of many generations, resulting in the decline of females. It is estimated that 28 generations are required to achieve complete introgression of the male-dominant daughterless carp construct into the population and that extinction of the population will occur in the range of 75–97 years (Brown and Walker 2004). The time frame of extinction will depend on the numbers of Trojan fish added but is similar between the daughterless carp strategy and the YY eradication strategy (i.e., decades).

Like the YY fish strategy, the daughterless carp strategy is specific for the target fish and therefore expected to have minimal impact on native fishes. However, the two strategies also share several disadvantages. For example, both strategies require a constant influx of the Trojan fish over many decades to achieve extinction; thus, neither strategy produces an immediate decrease in the population of carps in the system. Instead, an actively reproducing population of carps persists over the course of many decades (limited by the carrying capacity of the system) and eventually collapses only upon the elimination of females. The negative impacts of the carps therefore persist for the time course of the intervention. Additionally, both the daughterless carp strategy and the YY eradication strategy require a significant investment in technology to construct the Trojan fish.

To produce the daughterless carp Trojan fish, a functional aromatase inhibitor gene construct must be inserted into multiple carp chromosomes (ideally, all chromosomes), with each insertion representing a significant investment in time and labor. Not every insertion is expected to result in functional expression of the aromatase inhibitor, so each insertion must be individually characterized for expression and stability. Finally, genetic crosses between carps bearing different chromosomal insertions are required to combine the functional aromatase inhibitor genes located upon different chromosomes. The molecular characterization involved in constructing a Trojan fish with even only a few gene insertions is thus considerable. In addition to being laborious and time-consuming, the recombinant DNA technology used to construct the daughterless carp produces a transgenic organism intended for release into the environment, with all the potential associated risks (Muir and Howard 1999).

Although the YY Trojan fish can be constructed without the use of laborious genetic engineering (and would not involve the release of a transgenic organism into the environment), the current technology for producing YY carps is at a very early stage of development for all species of Asian carps, thus limiting its practical application. Two key procedures are essential to YY broodstock production, hormone-induced sex reversal and gynogenesis/androgenesis, each involving difficulties for Asian carp species (Shelton 2006). Estrogen-induced sex reversal in grass carp and silver carp cannot be easily achieved by feeding juveniles hormone-containing feed, as these species do not readily take feed. The difficulty associated with the sex reversal of grass carp and silver carp limit the usefulness of gynogenesis as a procedure to produce YY males from sex-reversed males (Fxy). Similar limitations will likely apply to bighead and black carp, which also do not accept feed readily (C.Engle, University of Arkansas at Pine Bluff, personal communication). To a limited extent, the problem of sex reversal of grass carp and silver carp can be solved by using hormone-containing silastic implants inserted into the fish gonad (Shelton 1986; Mirza and Shelton 1988), in this case reversing the sex of females to males with methyltestosterone. However, these procedures are laborious and have not been investigated as a means of estrogen-induced sex reversal.

As an alternative to gynogenesis, androgenesis has been used successfully in common carp as a procedure to produce YY males (Bongers et al. 1999). To confirm the Myy genotype, males that are produced by androgenesis must be crossed to tester females and the resulting progeny analyzed for the expected sex ratio (all male). Production of Fyy carps through androgenesis has not been investigated. However, the production of Fyy would necessarily require estrogen-induced sex reversal of juveniles (presumably via silastic implants) and mating tests of each fish to determine those containing the desired YY genotype. Although it is theoretically possible to produce the Myy and Fyy carp broodstock fish needed for the production of YY fish, the estrogen-induced sex reversal of large numbers of YY fish remains as a significant technological barrier, potentially limiting the production of Fyy carps at a large scale. Thus, additional experimental research will be required for each Asian carp species in order to assess the practicality of producing YY females. Further research is also needed to assess the efficiency of YY females mating and persistence relative to wild types before undertaking a YY eradication strategy directed towards Asian carps.

The YY eradication model presented indicates that extinction is a theoretical possibility within a riverine system. Although technical limitations currently limit the practical application of this strategy, the results suggest that further investigations into the technology of sex reversal and genetic manipulation of Asian carps through gynogeny are warranted. Further modeling of the effects of Trojan fish will be also be useful in understanding the kinetics of extinction using genetic approaches.

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