Eradicating Invasive Species Through Sex Reversal

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1 Introduction

An exotic species is a species that is not native to its current habitat and is known as invasive if it negatively impacts this habitat. There have been a variety of attempts to eradicate invasive species in different areas, but they have not been particularly successful. In an effort to find a better method for eradicating invasive fish species, Gutierrez and Teem proposed a method involving sex-reversal [2]. In 2001 it was discovered, in the Columbia River in the northwestern United States, that exposure to certain sex hormones can feminize XY fish, allowing them to reproduce [4]. Then when a feminized XY fish mates with a male XY fish, they can give birth to a YY fish, known as a supermale. Similarly, hormone exposure can feminize these YY supermales, allowing them to reproduce also.

Gutierrez and Teem's proposed eradication method involves the introduction of feminized supermales of an invasive species into a wild population. The feminized supermales will mate with the wild XY male fish and give birth to YY supermales. Thus there will be four different populations in this species: female XX, male XY, supermale YY, and the introduced feminized supermale YY. With these four populations, there are four different reproduction possibilities. The progeny from the mating of XX and XY is 1/2 XX and 1/2 XY, the mating of XY and the male YY produces 1/2 XY and 1/2 male YY, the mating of XX and male YY produces all XY progeny, and male YY and female YY mating produces only male YY. As the number of supermales and feminized supermales increases, the number of XX females born will decrease. The goal is to eventually eliminate all of the female fish so that when the addition of feminized supermales stops, the species will die out.

2 Methods

2.1 The Ordinary Differential Equations Model

The four reproduction possibilities dictate the ordinary differential equations (ODE) for each of the populations. Let f be the number of XX females of the targeted invasive species in the ecosystem, m be the number of XY males, s be the number of YY supermales, and rbe the the number of YY feminized supermales. The feminized supermales are added to the ecosystem at a constant rate μ . There is a birth coefficient β that represents the proportion of male/female encounters that produce viable offspring. The death coefficient δ represents the proportion of the population that dies in a unit time period. K is the carrying capacity of the ecosystem, and L is the logistic term that prevents the population from exceeding the carrying capacity, that is L = 1 - (f + m + r + s)/K. Using these parameters and the reproduction possibilities, Gutierrez and Teem developed the ODE model below.

$$\frac{df}{dt} = \frac{1}{2} fm\beta L - \delta f, \tag{1}$$

$$\frac{dm}{dt} = \left(\frac{1}{2}fm + \frac{1}{2}rm + fs\right)\beta L - \delta m,\tag{2}$$

$$\frac{ds}{dt} = (\frac{1}{2}rm + rs)\beta L - \delta s, \qquad (3)$$

$$\frac{dr}{dt} = \mu - \delta r. \tag{4}$$

The birth term of Equation 1 is $\frac{1}{2}fm\beta L$ because female fish are only produced from interactions between m and f, and β of these interactions result in progeny, half of which are female. Due to the L term, the number of births decreases as the ecosystem approaches its carrying capacity. Males make up half of the progeny between f and m, half of the progeny between r and m, and all of the progeny between f and s, so the birth term of Equation 2 is $(\frac{1}{2}fm + \frac{1}{2}rm + fs)\beta L$. The birth term of Equation 3 is $(\frac{1}{2}rm + rs)\beta L$ because half of the progeny between r and m and all of the progeny between r and s are supermale. Feminized supermales are not produced through mating, so the positive term is just μ , the rate at which feminized supermales are added to the ecosystem. The negative terms in each of the equations represent death, so they are δ , the rate at which fish of the given species die, multiplied by either the f, m, s, or r population. A numerical solution to the differential equations was found using the Runge-Kutta method [?].

A limitation of the ODE model is that the population of the invasive species will never reach zero in finite time, so we developed a stochastic model to more accurately model the elimination of an invasive species.

2.2 Continuous Time Stochastic Model

The stochastic model employed the Gillespie Algorithm, using the rates from the ODE model to determine the probabilities of the seven possible events. These seven events are a birth in the f, m, or s population and a death in the f, m, s, or r population [1]. Time between events is a continuous random variable that is exponentially distributed with mean equal to the sum of the seven event rates. Feminized supermales cannot be born naturally, but μ fish are added to the r population (as long as it doesn't exceed the carrying capacity) after each unit of time has passed. Rates of each event are shown in Table 1.

Event	Rate
f birth	$\frac{1}{2}fm\beta L$
m birth	$(\frac{1}{2}fm + \frac{1}{2}rm + fs)\beta L$
s birth	$(\frac{1}{2}rm + rs)\beta L$
f death	δf
\boldsymbol{m} death	δm
s death	δs
r death	δr

Table 1: Stochastic Rates

The probability of extinction under various scenarios was determined by running 100 trials and calculating the proportion of trials that will result in extinction, which is sure once f = 0.

2.3 Discrete Time Spatial Model

A spatial stochastic model does not assume that all fish are always uniformly distributed throughout their habitat. The habitat is divided into an $n \times n$ grid. Each type of fish has a certain probability of migrating to one of the four nearest neighboring cells. For diffusive migration, a fish of a given population will only migrate to a cell that has fewer of its population than its current cell has. There are at most 16 possible migration events for each cell of the grid, since there are four nearest neighbors for four different populations. There are still seven birth/death events for each cell, so for this method there are 24 possible events at each cell, where the 24th is the event that nothing changes in the discrete time period. At each time step it is determined which of the 24 events occurs in each cell. The cells update in a random order at each time step to eliminate any bias based on the order of cell update.

All models were impletmented in Matlab [3]. The following parameters were used for all of the trials in this paper: $\beta = 0.01$, $\delta = 0.1$, K = 300, and the initial female and male populations of 100. According to Gutierrez and Teem, β can vary between .01 and 10, and δ can vary between .1 and 3 [2].

3 Results

3.1 ODE Model

Starting with the number of feminized supermales added at each time unit set at some positive nonzero integer μ , the number of females in the habitat decreases over time. When the females reach a certain proportion of the overall population, one can stop the addition of feminized supermales. When $\mu = 0$, there are two locally stable equilibrium points and one unstable equilibrium point. It is important to look at both the male and female populations when $\mu = 0$ in order to determine whether the species will recover to the normal state stable equilibrium, where m = f or whether it approaches the elimination stable equilibrium.

The results indicate that when $\mu = 10$, the male and female populations recover when μ is set to zero as soon as the females make up 0.028 or more (with accuracy to the nearest hundredth) of the total population. Figure 1 shows the recovery when this proportion threshold is equal to 0.028. If one waits until the females make up 0.027 or a smaller proportion of the population before setting $\mu = 0$, then the species will proceed towards extinction, as shown in Figure 2. However, since this is an ODE model, the population will

never actually reach 0 in finite time.



Figure 1: ODE solution where $\mu = 0$ when females make up 0.028 of the total population.



Figure 2: ODE solution where $\mu = 0$ when females make up 0.027 of the total population.

3.2 Stochastic Model

One hundred trials of the stochastic model were run with $\mu = 5$, $\mu = 10$, and $\mu = 15$, and with a range of different proportions of the overall population that f must reach before setting $\mu = 0$. Figure 3 displays the probability that the population will go extinct (given a sufficient amount of time) for the proportion values between 0 and 0.1.

Figure 4 shows the average time to the point where μ is set to zero for the same set of



Figure 3: Probability of extinction, where $\mu = 0$ when the females make up a certain proportion. of the total population

100 simulations. It takes significantly longer to get to this point when $\mu = 5$ than when $\mu = 10$ or $\mu = 15$. The time change is slow between the female proportion of 0.04 and 0.1, so it only requires a small time cost to wait until the females get to a smaller proportion of the population, in order to maximize the probability of extinction.



Figure 4: Average time to the point where $\mu = 0$, given that this occurs when the females make up a certain proportion of the total population.

Figure 5 shows the average time to extinction, given that $\mu = 0$ as soon as the females decrease to a certain proportion of the species population. The variance of this data was greater than the average time to $\mu = 0$, and there are fewer data points when the proportion is higher, since not fewer trials result in extinction.



Figure 5: Average time to extinction, given that $\mu = 0$ when the females make up a certain proportion of the total population.

3.3 Spatial Model

Based on observations of the spatial model, if the sum of the male and female population is close to the carrying capacity, then it is very unlikely that the species will go extinct. Extinction is unlikely because the feminized supermales and supermales do not have enough space to increase dramatically. Such a dramatic surge is necessary to drive the female population down toward the desired proportion. Similarly, the value of μ must be high enough to give the feminized supermales a foothold. Otherwise they will not reproduce a sufficient number of supermales to outnumber the males and females. It seems as though it is more productive to add a large number of feminized supermales for a shorter amount of time than to add fewer fish for a longer period of time. The latter option will be less successful because there will not be enough of the feminized supermales to migrate and sustain their population throughout the grid.

4 Discussion

The results of this study provide further insight into the effectiveness of the Trojan Y Chromosome Model by looking at the model from a stochastic perspective. This more realistically models the eradication strategy because it uses integer populations and allows for the possibility of extinction in finite time. The spatial element extends the model so that an invasive species can be eradicated from a larger area. The results show that given a desired probability of extinction and time to extinction, one should wait until the females make up a specific proportion of the population.

It would be of interest to look into variations of the spatial model. In this model the feminized supermales are always added to the same cell each time, so often that corner acts like the non-spatial stochastic model, where the increase in feminized supermales leads to a reduction in females. However, if the surrounding cells are near the carrying capacity, then the feminized supermales are not able to migrate very successfully, so the female population will remain high in most of the grid. It would be interesting to see the effects of adding the feminized supermales to multiple cells at one time or rotating which cell they are added to.

In addition the spatial model was most successful when a large number of feminized supermales were added to the ecosystem at first so that the increase in feminized supermales and resultingly in supermales would drive the female and male population down quickly. If μ is not large enough and the female and male populations increase towards the carrying capacity, then there is no longer an opportunity for extinction. This is due to the way this model was constructed. In this model the addition of feminized supermales and the migration events cannot surpass the cell's carrying capacity. It would be interesting to vary the model so that these processes can surpass the carrying capacity, and then the migration and death events would drive the population back down to carrying capacity. One way to implement this would be through a logistic delay equation so that the rates are calculated using populations from a previous time. This may provide more interesting results and a greater probability of extinction.

Finally, another variation to explore would be the a continuous time spatial model, which would be more comparable to the non-spatial stochastic model. This would again use the Gillespie Algorithm, so the time would update whenever one event occurred in the entire grid. Thus for an $n \times n$ grid, there would be $24 \times n \times n$ possible events at each step. This may be more accurate than using a constant time step because in reality dt should vary based on the current population. We hope that this research will help make this TYC eradication strategy a reality in the future so that we can reduce the negative impacts of invasive species on their aquatic habitats.

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