Ecological Modelling 361 (2017) 14–25

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

An integral projection model with YY-males and application to evaluating grass carp control

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ARTICLE INFO

Article history:
Received 21 April 2017
Received in revised form 25 July 2017
Accepted 27 July 2017
Available online 4 August 2017

Keywords:
Asian carp
Fisheries management
Cyprinidae
Great Lakes
Lake Erie
Invasive species

ABSTRACT

Invasive fish species disrupt ecosystems and cause economic damage. Several methods have been discussed to control populations of invasive fish including the release of YY-males. YY-males are fish that have 2 male chromosomes compared to a XY-male. When YY-males mate, they only produce male (XY) offspring. This decreases the female proportion of the population and can, in theory, eradicate local populations by biasing the sex-ratio. YY-males have been used as a population control tool for brook trout in montane streams and lakes in Idaho, USA. The YY-male control method has been discussed for grass carp in Lake Erie, North America. We developed and presented an integral projection model for grass carp to model the use of YY-males as a control method for populations in this lake. Using only the YY-male control method, we found that high levels of YY-males would need to be release annually to control the species. Specifically, these levels were the same order of magnitude as the baseline adult population (e.g., 1000 YY-males needed to be released annual for 20 years to control a baseline adult population of 2500 grass carp). These levels may not be reasonable or obtainable for fisheries managers given the impacts of YY-males on aquatic vegetation and other constraints of natural resource management.

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1. Introduction

Over the last two decades, numerous invasive fishes have established populations throughout the United States including grass carp (*Ctenopharyngodon idella*). Different control techniques have been discussed to control populations of these species either through direct mortality or reduction of their spread. Possible control methods include acoustical conditioning (Sloan et al., 2013), new piscicides (Putnam et al., 2017), commercial harvest (Colvin et al., 2012), carbon dioxide barrier (Cupp et al., 2016; Donaldson et al., 2016), and the release of YY-males that only produce male offspring (Schill et al., 2016). The YY-male approach controls populations because YY-males can only produce male offspring. If enough YY-males are in the population, the sex-ratio can become biased sufficiently that the population may collapse or be more vulnerable to other control efforts. YY-males have recently been used in montane streams and lakes in Idaho to attempt to control invasive brook trout (Schill et al., 2016). Similar management approaches have been used for other invasive and noxious species such as mosquitoes (Benedict and Robinson, 2003) although not without controversy or challenges (c.f. Knols et al., 2006). We are specifically interested in the release of YY-males for grass carp control because the method has been discussed for controlling grass carp in Lake Erie, North America.

Grass carp, like many invasive fishes, cause a wide-range of adverse economical and ecological impacts in North America (Lovell and Stone, 2005; Dibble and Kovalenko, 2009). Directly, grass carp can consume up to 40% of their weight in vegetation daily, which alters available habitats, water quality, and community composition (Sutton, 1977; Chapman et al., 2013). Indirectly, grass carp adversely affect other species ranging from plankton to waterfowl (Bain, 1993; Kolar and Lodge, 2002; Dibble and Kovalenko, 2009). These ecological impacts cause economic impacts such as declines in native fisheries and contribute to the billions of dollars of damage that invasive species cause to the economy of the United States (Pimentel et al., 2000, 2005).

Grass carp originated in eastern Asia; its native range spans from the Amur River of Russia to the West River of southern China

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http://dx.doi.org/10.1016/j.ecolmodel.2017.07.030
0304-3800/Published by Elsevier B.V.

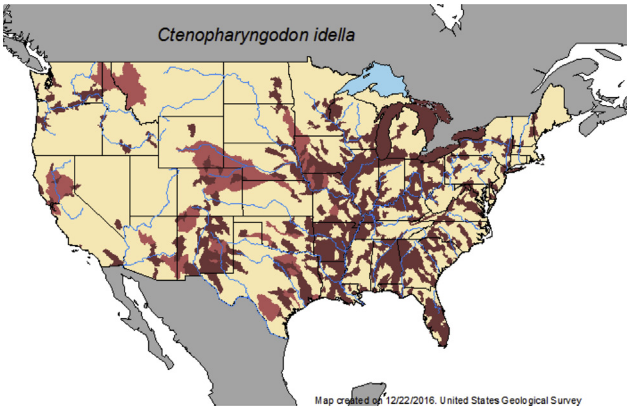

Fig. 1. Species distribution map of grass carp (*Ctenopharyngodon idella*) in the continental United States. Darker shading areas are observations from HUC 8 Level records, lighter are from HUC 6 Level Records. Map is was generated by the USGS on 22 December 2016 and accessed 23 January 2017 (https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=514). The figure was created by Nico, L.G., P.L. Fuller, P.J. Schofield, M.E. Neilson, A.J. Benson, and J. Li while working for the U.S. Government and is in the public domain.

(Shireman and Smith, 1983). The species feeds on aquatic vegetation and has been introduced worldwide for weed control including Malaysia, Taiwan, Japan, eastern Europe, Holland, Germany, New Zealand, and the United States (Cross, 1969; Clayton et al., 1999). First proposed for release in the United States in 1957 to control aquatic vegetation (Swingle, 1957), natural resource managers released the species 6 years later in 1963 (Bain, 1993; Mitchell and Kelly, 2006). Grass carp spread through flooding in stocked areas and additional stocking and now may be found in the Great Lakes (Chapman et al., 2013) and Mississippi River Basin(Bain, 1993) (Fig. 1).

Early studies of grass carp examined how to use the species for weed control and increase survival and recruitment of grass carp (e.g., Cross, 1969; Sutton, 1977; Mitzner, 1978; Kilambi and Robison, 1979; Ewel and Fontaine, 1982; Martyn et al., 1986; Rottmann et al., 1991; Santha et al., 1991; Spencer, 1994). Managers and scientists in the United States noticed the adverse impacts of the species and began releasing sterile, triploid grass carp as a method for limiting their adverse impact (Chilton and Muoneke, 1992). However, many viable, reproducing populations still exist throughout the United States (Raibley et al., 1995; Wittmann et al., 2014; Embke et al., 2016). Currently, some grass carp management focuses on control (Chapman et al., 2013; Wittmann et al., 2014), although regions still stock grass carp for vegetation control.

Prior to developing and implementing possible control methods, researchers and managers may want to evaluate the effectiveness of the approaches. Ecological simulations using mathematical models are one approach to compare different management methods (Caswell, 2001; Morris and Doak, 2002; Bolker, 2008). Additionally, mathematical theory can be used to “optimize” management (Lenhart and Workman, 2007), “control” the system (Friedlan, 1986), or compare different management strategies (Caswell, 2001; Morris and Doak, 2002).

Several different mathematical population models have been developed for invasive carp (e.g., silver carp, bighead carp, common carp; Lorenzen, 1995; Williamson and Garvey, 2005; Garcia et al., 2013; Tsehaye et al., 2013; Cuddington et al., 2014) including grass carp (Ewel and Fontaine, 1982; Santha et al., 1991; Spencer, 1994; Kirk et al., 2000). The life history of carp is conserved within the family Cyprinidae and these models could be re-parameterized for grass carp. Furthermore, Lorenzen (1995) presented a generic fisheries model that includes carps as an example species. However, these models do not match our management questions. First, the models tend to be designed for specific locations and questions that differ from ours (e.g., how to release grass carp for weed control). Second, none of these models differentiate carp by sex nor do they include YY-males. Third, some of the models (e.g., Kirk et al., 2000) do not include sufficient details to easily reproduce the model, highlighting the need for documentation (c.f. Schmolke et al., 2010; Augusiak et al., 2014).

Like most fish, carp grow continuously and change in size through time. Conversely, many of the existing models were difference equations or differential equations that discretized carp size using life-stages rather than size (e.g., Lefkovitch matrix models); model age as a surrogate for size and thereby implicitly discretize size (e.g., Leslie matrix models), or completely ignored size/age structure in the carp populations. Rather than discretizing size, size can be modeled continuously using an integral projection model (Easterling, 1998; Ellner and Rees, 2006; Ramula et al., 2009; Merow et al., 2014). These models were first applied to population ecology by Easterling (1998) during his graduate work and offer advantages over matrix models when modeling discretized systems (e.g., size classes). First, integral projection models require fewer parameters than a discrete matrix of similar complexity. For example, rather than estimating a survival parameter for each life-stage, one function with two parameters can be fitted to model survival as a function of size (Easterling et al., 2000; Ellner and Rees, 2006). Second, integral projection models avoid modeling errors and artifacts caused by the choice of size structures. For example, Easterling et al. (2000) demonstrated how arbitrary choices in the number of size classes change the transient dynamics and long-term behavior of models. Integral projection models avoid this pitfall by treating size as a continuous variable rather than discretizing it.

Herein, we develop an integral projection model for grass carp that includes XX-females, XY-males, and YY-males. After presenting our model and its parameterization, we conduct sensitivity analysis and compare different possible management scenarios to evaluate the possible use of YY-males. We include our “TRAnsparent and Comprehensive model Evaludation[1]” (TRACE) Documentation as a supplemental document (Schmolke et al., 2010; Augusiak et al., 2014; Grimm et al., 2014).

2. Model

2.1. Grass carp life history

Grass carp broadcast spawn in rivers, and their eggs must remain suspended in the water column until larvae are sufficiently developed to swim freely (Shireman and Smith, 1983). Males appear to have YX chromosomes and females have XX chromosomes (Wang et al., 2015). The specific requirements for successful spawning and recruitment (e.g., temperature, river discharge, and dissolved oxygen) constrain the spread of grass carps in systems such as the Great Lakes (Kocovsky et al., 2012). However, aquaculture techniques exist for spawning grass carp in captivity (e.g., Rottmann et al., 1991). We define recruitment to be from hatching until age-1 fish based upon the annual time step of our model (i.e., $t = 1$ year). Grass carp, like most species of fish, experience indeterminate growth and continue to grow throughout their life (Lagler et al., 1962). Grass carp do not reproduce until their body reaches an adequate size (Shireman and Smith, 1983). We modeled this using length as the state variable (Fig. 2). Grass carp mortality decreases as the fish increase in size because the carp are less vulnerable to predation and other stressors (Shireman et al., 1978; Shireman

[1] “Evaludation” was intentionally invented by Grimm to cause the reader to think about the term, (V. Grimm, personal communication).

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