Ecological Modelling 387 (2018) 163–171

Contents lists available at ScienceDirect

Ecological Modelling

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

A spatially discrete, integral projection model and its application to invasive carp

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ARTICLE INFO

Keywords:
Fisheries management
Invasion ecology
Population dynamics
Network-node
Spatial model

ABSTRACT

Natural resource managers and ecologists often desire an understanding of spatial dynamics such as migration, dispersion, and meta-population dynamics. Network-node models can capture these salient features. Additionally, the state-variable used with many species may be appropriately modeled as a continuous variable (e.g., length) and management activities sometimes can only target individuals of certain sizes. Integral projection models (IPMs) can capture this life history characteristic and allow for the examination of size-specific management. We combined an IPM with a network-node model to capture both of these salient features. We then demonstrated how this model could be used to understand and manage populations of invasive species focusing on grass carp as an example. Grass carp disrupt ecosystems outside of their native range and have spread around much of the world, including North America. The impacts of grass carp include adversely changing aquatic plant communities, which in turn affect a wide range of endpoints ranging from water quality to waterfowl recruitment. We specifically examined two theoretical systems using parameters from the literature. First, we modeled a lake with two tributaries and examined how modified sterile males could be used as a control tool. We found that modified sterile males may be a feasible control tool to limit population growth. Second, we modeled a series of river pools and examined how harvest and deterrents could be used to decrease the risk of expanding grass carp's range within a river system. Within this system, we also compared the impacts of size specific harvest and uniform harvest across all sizes. We found that targeting the largest, spawning populations may be more important than targeting the populations close to the invasion front for reducing the risk of spreading grass carp. We also demonstrate that size of harvested fish was important for controlling populations.

1. Introduction

Understanding both size-specific demographics (i.e., how the size-distribution of individuals within a population impacts the population's dynamics; Easterling, 1998) and spatial dynamics (i.e., the movement and migration of organisms between habitats; Bowlin et al., 2010) can be important for both basic ecology and conservation management. In the past two decades, advances have been made in population ecology to better understand both size-specific and spatial dynamics. Specifically, integral projection models (IPMs) have emerged as an approach for modeling organisms with continuous state-variables (e.g., organism size) in contrast to discrete state-variables (e.g., using life-stages such as juveniles and adults) (Easterling, 1998; Ellner and Rees, 2006) and network-node-based full-annual cycle (FAC) models have emerged as an approach for modeling spatially discrete populations (Taylor and Norris, 2010; Hostetler et al., 2015). We merged both of these approaches to model an invasive species, grass carp (*Ctenopharyngodon idella*), and then compare invasive species management scenarios. In the remainder of the introduction, we provide an overview of how grass carp represent other aquatic invasive species as well as describe how IPMs may be combined with network-node-based FAC models to capture the biology and management of grass carp.

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https://doi.org/10.1016/j.ecolmodel.2018.09.006
Received 27 February 2018; Received in revised form 5 September 2018; Accepted 7 September 2018
0304-3800/ Published by Elsevier B.V.

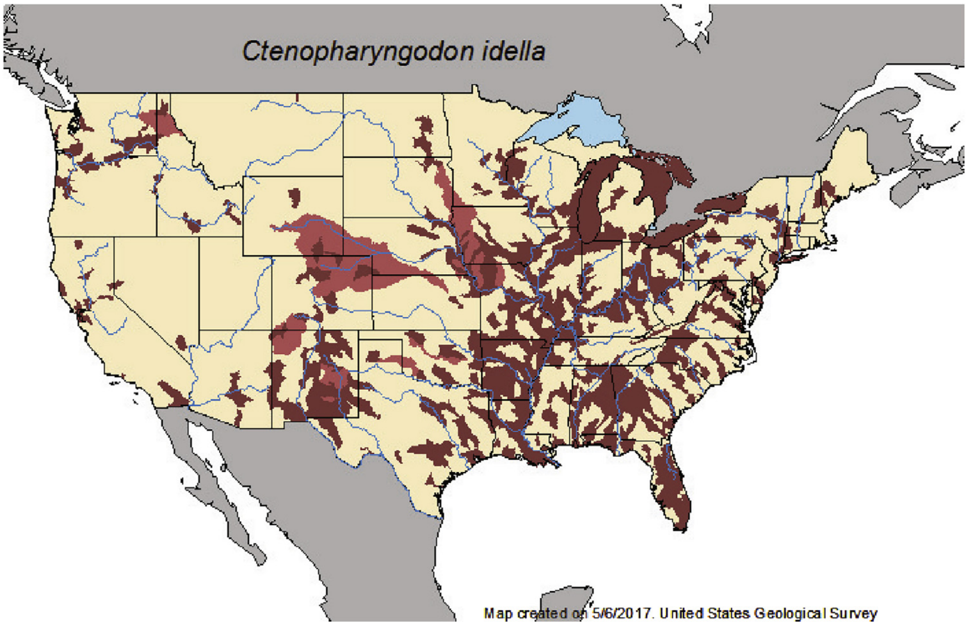

Fig. 1. Species distribution map of grass carp (*Ctenopharyngodon idella*) in the continental United States. Darker shaded areas are observations from Hydrological Unit Code (HUC) 8 Level records, lighter shaded areas are from HUC 6 Level Records. The map was generated by the USGS on 6 May 2017 and accessed 28 July 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.

Grass carp have many traits and an introduction history that make them representative of other aquatic invasive species. Natural resource managers initially introduced the species in North America, specifically to control vegetation in aquaculture facilities, wastewater treatment facilities, and energy production centers (Swingle, 1957; Shireman and Smith, 1983; Bain, 1993; Mitchell and Kelly, 2006). After the initial release, flooding combined with additional stocking and reproduction in the wild allowed the species to spread to both the Great Lakes (Chapman et al., 2013) and the Mississippi River basin (Bain, 1993) (Fig. 1). Like many other invasive species, grass carp cause large scale economic and ecological damage outside of their native range and concern exists about range expansion in North America (Kolar and Lodge, 2002; Cuddington et al., 2014; Lodge et al., 2016; Zhang et al., 2016). Specific impacts of grass carp include altering aquatic vegetation and plankton communities and reducing water quality, which ultimately displace native fishes, vegetation, waterfowl, and disrupt their interconnected community structure and assemblage (Kolar and Lodge, 2002; Irons et al., 2007; Sass et al., 2014; Lodge et al., 2016; Zhang et al., 2016).

The ecology and life history of grass carp can be described using a network-node FAC modeling framework. Populations of grass carp such as those in Lake Erie exhibit seasonal migration between the lake and its tributaries, with spawning occurring in the tributaries and the fish spending most of their life in the lake (Chapman et al., 2013). This seasonal migration makes capturing the FAC across discrete habitats important for modeling efforts. Populations such as those in the Mississippi River basin can only spawn in certain pools of the rivers because fertilized eggs must remain suspended until the larvae develop the ability to independently swim (Shireman and Smith, 1983). This different use of discrete habitats makes consideration of metapopualtion dynamics important, something network-node models can capture well.

The ecology and life history of grass carp can be described using an IPM-framework as well. Many species of fish grow throughout their life, with growth slowing down asymptotically as fish increase in size (Isely and Brabowski, 2007) including grass carp (Shireman and Smith, 1983) Furthermore, grass carp demographic vital rates change as a function of size and larger carp are less likely to die and more likely to spawn (Shireman and Smith, 1983). In fact, we previously used an integral projection (Erickson et al., 2017b) to capture these salient growth features, but did not include any spatial structure as part of that model.

To reduce the impact and spread of grass carp, researchers and managers are actively attempting to develop new control methods. Proposed control efforts include applying acoustical conditioning (e.g., Sloan et al., 2013), developing new, carp specific piscicides (e.g., Putnam et al., 2017), harvesting by commercial fishers (e.g., Colvin et al., 2012), poisoning with carbon dioxide under ice (e.g., Cupp et al., 2017), slowing dispersal with carbon dioxide barriers (e.g., Cupp et al., 2016; Donaldson et al., 2016), releasing YY-males that only produce male offspring (e.g., Gutierrez and Teem, 2006; Teem and Gutierrez, 2011; Schill et al., 2016; Erickson et al., 2017b), and releasing genetically modified males that produce non-viable offspring (similar to mosquito releases described by Benedict and Robinson, 2003). The last two options are the most theoretical and have yet to be developed for grass carp. YY-males fish can be produced by using conventional technology such as feminizing XY-males and then breeding them with normal XY-males (Schill et al., 2016). Sterile males can be created using synthetics biology, using tools such as gene knockouts or gene additions (Benedict and Robinson, 2003). Additional demographic attributes of these resulting organisms, could, in theory, be modified. For example, one could increase the chance of modified fish spawning compared to non-modified organisms or decrease the lifespan of modified fish compared to non-modified organisms.

Many of these management tools are either size specific, which fit well into IPM-based models, or spatially explicit, which tie into an FAC network-node based modeling approach. For example, the barrier deterrents could be used to either limit spread of invasive species or disrupt the connectivity of existing subpopulations. The barriers hold potential in river systems such as the Upper Mississippi River basin that are fragmented by locks and dams (Chick et al., 2006). Conversely, understanding the FAC is important in deciding when, where, and how much of other management actions need to be done. For example, when and where should harvest be done and how much harvest is necessary to control a species? Many of these management actions are also size specific. Commercial harvest often can only target fish of certain sizes (Colvin et al., 2012) and toxicants can often vary in toxicity based upon the size of targeted individuals. The use of modified organisms through synthetic biology could also have size-specific considerations.

We developed this model because resource managers are concerned about the impact of grass carp if the population increases in size or expands its range. Furthermore, resource managers would like to be able to evaluate management scenarios and control tools for the species