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Biological Conservation

Modeling the fish community population dynamics and forecasting the eradication success of an exotic fish from an alpine stream

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ABSTRACT

Management actions aimed at eradicating exotic fish species from riverine ecosystems can be better informed by forecasting abilities of mechanistic models. We illustrate this point with an example of the Logan River, Utah, originally populated with endemic cutthroat trout (*Oncorhynchus clarkii utah*), which compete with exotic brown trout (*Salmo trutta*). The coexistence equilibrium was disrupted by a large scale, experimental removal of the exotic species in 2009–2011 (on average, 8.2% of the stock each year), followed by an increase in the density of the native species. We built a spatially-explicit, reaction-diffusion model encompassing four key processes: population growth in heterogeneous habitat, competition, dispersal, and a management action. We calibrated the model with detailed long-term monitoring data (2001–2016) collected along the 35.4-km long river main channel. Our model, although simple, did a remarkable job reproducing the system steady state prior to the management action. Insights gained from the model independent predictions are consistent with available knowledge and indicate that the exotic species is more competitive; however, the native species still occupies more favorable habitat upstream. Dynamic runs of the model also recreated the observed increase of the native species following the management action. The model can simulate two possible distinct long-term outcomes: recovery or eradication of the exotic species. The processing of available knowledge using Bayesian methods allowed us to conclude that the chance for eradication of the invader was low at the beginning of the experimental removal (0.7% in 2009) and increased (20.5% in 2016) by using more recent monitoring data. We show that accessible mathematical and numerical tools can provide highly informative insights for managers (e.g., outcome of their conservation actions), identify knowledge gaps, and provide testable theory for researchers.

1. Introduction

Biological invasions are one of the principal causes of declines in biodiversity, a stressor exacerbated by destruction of habitat, pollution, climate change and overexploitation of living resources (Millennium Ecosystem Assessment, 2005). The loss of biodiversity caused by exotic species notably results from competition, hybridization or predation on native species (Kraus, 2015). Furthermore, biological invasions are responsible for the alteration of ecosystem function and services, and can cause important economic losses (Gutierrez et al., 2014; Walsh et al., 2016).

Strategies for managing exotic species are diverse, depending on species and geography, and include, for instance, the use of biocides or other disturbance events such as wildfire, the use of natural enemies of exotic species, and harvesting, capturing or trapping methods (Knapp and Matthews, 1998; Nordström et al., 2003; Knapp et al., 2007;

Kettenring and Adams, 2011; Pluess et al., 2012; Gaeta et al., 2014; Saunders et al., 2014). Eradication (i.e., elimination of a exotic species from a given area) can often be set in action, at a cost (Fraser et al., 2006). However, in practice, eradication is still largely empirical, and management success is highly variable (Sheley et al., 2010). Eradication attempts not only fail to reduce the demography of exotic species, but can even lead to an increase in the abundance and distribution of the invasive species (the so-called 'hydra effect'), due to age- or density-dependent overcompensation processes, as shown for plant, insect, and fish populations (reviewed by Zipkin et al., 2009 and Abrams, 2009). To avoid such problems, and also the long-term costs of recurrent management, the eradication of exotic species can be targeted on specific locations or life stages (Maezono and Miyashita, 2004; Syslo et al., 2011; Hill and Sowards, 2015). Successful eradications have been reported for a wide range of organisms (see Pluess et al. (2012) for a review). Various factors influence the feasibility and cost-effectiveness

of exotic eradication, including biological traits of organisms, their limitation to some habitats (e.g. man-made habitats) and the timing of eradication attempt relative to the time the invasion started (Fraser et al., 2006; Pluess et al., 2012).

Although a global unifying theory is still lacking, several modeling approaches have proved to be useful to predict the distribution of invasive species (reviewed by Higgins and Richardson, 1996; Gallien et al., 2010; Hui et al., 2011). Some attempts have been made to predict the 'invasiveness' of organisms, as well as the invasibility of ecosystems (Barrat-Segretain et al., 2002; Hovick et al., 2012; Szymura et al., 2016). General concepts from community ecology can also be used for invasive species, and their distributions can be predicted, for example, using empirical habitat suitability models or by niche modeling based on species attributes (Thuiller et al., 2005; Buisson et al., 2008; Sharma et al., 2011; Marras et al., 2015). Similarly, invasion dynamics can be simulated by using mechanistic models. This latter modeling approach is also capable of providing a forecast of the species distribution once invasion draws to a close. Several mathematical frameworks have been considered for that purpose: individual based models which simulate dynamics based on rules for individuals (Prévosto et al., 2003; Nehrbass et al., 2006), metapopulation models which consider individual movements between spatially separated subpopulations (Hanski, 1998), cellular automatas which consider rules at the spatial unit scale with finite sets of states (Balzter et al., 1998; Vorpahl et al., 2009), and reaction-diffusion models based on partial differential equations (PDE) either in their continuous form or discretized and approximated by finite-difference (Okubo et al., 1989; Holmes et al., 1994; Hui et al., 2011). It is generally accepted that models need to be spatially-explicit in order to account for spatial heterogeneity of species density and/or of environmental factors (Holmes et al., 1994; Perry and Bond, 2004; Rammig and Fahse, 2009). Still, the superiority of mechanistic models lies in their ability to represent complex systems with a limited number of key attributes (e.g., parsimony), which results in scenario simulation (e.g., eradication action) and the ability to extrapolate to other systems.

Freshwater fish are one of the most common species introduced worldwide, and the ecological impacts of exotic freshwater fishes operate from genetic to ecosystem levels (Cucherousset and Olden, 2011). Among freshwater fish, salmonids are the most introduced organisms worldwide with varying impacts on native fish depending on the ecosystem, fish community, and ecological integrity (Krueger and May, 1991; Korsu et al., 2010). In many cases, invasive salmonids are detrimental to native salmonid populations due to the negative effects of competition and predation (e.g., Morita et al., 2004). Generally, this overlap leads to a decline of the native species and a decrease in population growth (herein and after, 'growth' means population growth), density, and survival (Benjamin and Baxter, 2012; van Zwol et al., 2012; Houde et al., 2015; Hoxmeier and Dieterman, 2016). More commonly, however, the negative effects of hatchery or exotic trout on native results in habitat segregation (e.g., Heggenes and Saltveit, 2007) that are often then expressed as strong longitudinal patterns of allopatric species distributions (reviewed in Budy and Gaeta, 2017). In this case native trout often choose or use different habitat in allopatry versus sympatry with exotic trout (e.g., Glova, 1987).

Brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) are two of the most pervasive and successful invaders worldwide and are ubiquitous across the Intermountain West (IMW), USA (Mcintosh et al., 2011). Brown trout is the foundation of extremely popular and economically significant sport fisheries, despite well-established negative effects on native fishes and ecosystems. This paradox results in very challenging, and often opposing, conservation and management goals (Budy and Gaeta, 2017).

Our objective in this paper is to illustrate that spatially-explicit, mechanistic models, even simple ones, are very useful tools to guide management efforts aimed at eradicating exotic fish species from riverine ecosystems. We illustrate this presentation with the study of the Logan River, Utah, which currently sustains one of the largest

remaining meta-populations of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*). However, lower elevation reaches of the watershed are dominated by exotic brown trout (*Salmo trutta fario*) (Budy et al., 2007, 2008; Mcintosh et al., 2011). The Logan River is in several ways ideal as a case study to fulfill our objective because (1) the Logan River was the site of a large-scale experimental mechanical removal of exotic brown trout in 2009–2011 (Saunders et al., 2014), (2) the Logan River has been monitored since 2001 thus providing quantification of abundance and distribution of both trout species before, during, and after the mechanical removal, and (3) the Logan River has been intensively studied including quantification of vital rates and population trend (Budy et al., 2007, 2008), competition and predation experiments and modeling at large and small, controlled scales (McHugh and Budy, 2005; Meredith et al., 2015), and attempts to better understand the role of the longitudinal gradient in physical factors on the distribution and abundance of native and exotic trout (De La Hoz Franco and Budy, 2005; Meredith et al., 2017).

Data are presented first, followed by a short preliminary statistical analysis, which highlights some major aspects of the system under study. We then present a spatially-explicit, mechanistic model of brown trout and cutthroat trout growth, dispersal, and competition. The model is first calibrated, and as a second step is used to make a forecast of the outcome of the 2009–2011 mechanical removal. Notably, it is important to stress out that we follow a top-down approach, starting with a simple model which provides an integrated view of the system's working. We then model processes with more details, and discuss the strengths and weaknesses of the latter in the discussion. Such a discussion allows us to highlight knowledge gaps and make suggestions for future data collection and modeling efforts. The discussion ends with the consideration of models to guide management efforts aimed at eradicating exotic fish species from riverine ecosystems.

2. Material & methods

2.1. Study area and data collection

2.1.1. Study area

The Logan River originates in southeastern Idaho in the Bear River Mountain Range and continues to its confluence with the Bear River in northern Utah. The climate throughout the Logan River watershed is characterized by cold snowy winters and hot, dry summers. Winter ice formation, specifically anchor ice, is also prevalent in high elevation stream reaches. As a result, the hydrograph is dominated by spring snowmelt floods (ca. $16 \, m^3.s^{-1}$) and base flow conditions (ca. $3 \, m^3.s^{-1}$) that persist from August to April. Average summer temperatures range from approximately 9°C (headwaters and tributaries) to 12°C (mid-elevation mainstem), and diel fluctuations are up to 9°C (De La Hoz Franco and Budy, 2005). Above a series of small low elevation dams in the lower river, there are no barriers to fish movement in either the upstream or downstream direction, and the river is characterized as high quality, connected habitat (Mohn, 2016).

2.1.2. Fish community

As noted earlier, the Logan River sustains one of the largest remaining meta-populations of endemic Bonneville cutthroat trout (*Oncorhynchus clarkii utah*). However, this sub-species of native trout has experienced range-wide reductions in abundance and distribution due to the usual suspects of habitat degradation, reduced connectivity, exotic parasites, and the negative effects of exotic species. Cutthroat trout compete with exotic brown trout (*Salmo trutta fario*) which occur in some of the highest densities reported in the world (Budy et al., 2007, 2008; Mcintosh et al., 2011). Exotic brown trout were historically stocked, largely in the lower river, starting in the 1800's and propagule pressure was quite high (Budy and Gaeta (2017); but see Meredith et al. (2017)). In addition to endemic Bonneville cutthroat trout and exotic brown trout, resident fish in the Logan River include stocked rainbow