Ecological Modelling 296 (2015) 79–92

Contents lists available at ScienceDirect

Ecological Modelling

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

Spatiotemporal variation in flow-dependent recruitment of long-lived riverine fish: Model development and evaluation

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ARTICLE INFO

Article history:
Received 26 June 2014
Received in revised form 18 October 2014
Accepted 20 October 2014
Available online 7 November 2014

Keywords:
River
Population dynamics
Energetics
Individual-based models
Spatially explicit models
Shovelnose sturgeon
Conservation

ABSTRACT

Natural flow regimes can play a major role as an overarching ecosystem driver in reproduction and recruitment of riverine fishes. Human needs for freshwater however have altered hydrology of many riverine systems worldwide, threatening fish population sustainability. To understand and predict how spatiotemporal dynamics of flow regimes influence reproductive and recruitment variability, and ultimately population sustainability of shovelnose sturgeon (*Scaphirhynchus platorynchus*), we develop a spatially explicit (1D) individual-based population model that mechanistically (via energetics-based processes) simulates daily activities (dispersal, spawning, foraging, growth, and survival). With field observations of sturgeon and habitat conditions in a major tributary of the Missouri River system (USA), we calibrate and evaluate the model via pattern-oriented modeling. Model simulation experiments using 17-year environmental time series data showed that seasonal and interannual variation in hydrological conditions plays a major role in timing, location, and magnitude of spawning and recruitment success of sturgeon. During droughts, consecutive weak year-classes resulted in a steady population decline. While low flow and subsequent low prey production limited foraging opportunities and slowed gonad development, these conditions were not severe enough for adults to abort the reproductive cycle. Post-settlement larval sturgeon were however unable to feed efficiently to grow out of a size-dependent 'predation window', resulting in high mortality. Slow growth and low survival of larval sturgeon thus likely play a larger role in recruitment failures during droughts than low or lack of spawning events.

1. Introduction

Life history strategies of organisms have evolved by adaptation to the natural variability of environmental drivers (Hutchings, 2002; Lytle and Poff, 2004; Winemiller and Rose, 1992). Consistent availability of natural habitats suitable for reproduction and recruitment is therefore essential in maintaining sustainable populations (Gibson, 1994). A variety of human activities have however facilitated habitat degradation and destruction, threatening population sustainability of many species in aquatic and terrestrial systems (Lucas and Marmulla, 2000). Understanding underlying mechanisms driving environment–life history trait relationships for populations under environmental stress is thus becoming increasingly important for conservation and management in these systems (Hampe and Petit, 2005).

In riverine systems, the natural flow regime can play a critical role in reproduction and recruitment of aquatic and terrestrial organisms (Humphries et al., 1999; Nunn et al., 2007), and ultimately in structuring community assemblages and functioning as an overarching ecosystem driver (Bunn and Arthington, 2002; Lytle and Poff, 2004). Human needs for freshwater however have made substantial impacts on hydrology and geomorphology of many riverine systems worldwide (Nilsson and Berggren, 2000). Many of these systems have been channelized to regulate the flow; regulated systems usually have less capacity to buffer perturbations (e.g., droughts) than natural systems (Palmer et al., 2008). Flow regulation for instance has altered life-history traits of fish species, resulting in persistent recruitment failures and threatening sustainability of populations in these systems (Bunn and Arthington, 2002; Poff et al., 1997).

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http://dx.doi.org/10.1016/j.ecolmodel.2014.10.026
0304-3800/

Recruitment variability in fish is often regulated by environmental drivers (e.g., water temperature) that affect growth and survival during early life stages (Anderson, 1988; Houde, 1987, 2009). Cyclic prey population dynamics linked with environmental variability during the transition to the feeding stage ('critical period') has been hypothesized as a dominant driver of recruitment success (Cushing, 1996; Humphries et al., 2013); specifically, survival of larval fish may depend on fast growth via consistent foraging success to avoid size-dependent predation (Houde, 2009).

While a number of studies have examined the roles of biological and environmental drivers in foraging success and ultimately recruitment in marine systems (Boehlert and Mundy, 1988), underlying mechanisms of recruitment success for riverine fishes (i.e., flow–recruitment relationships) is less understood (Bunn and Arthington, 2002; Lytle and Poff, 2004). For riverine fishes, flow regime changes in spawning and rearing grounds may bring about changes in temperature regime and food availability that could disrupt early life stage processes such as timing and location of spawning and settlement (Humphries et al., 1999; King et al., 2003; Nunn et al., 2007).

River flow may also indirectly influence recruitment success via energetics and maturation processes in juvenile and adult females that ultimately determine reproductive output (Encina and Granado-Lorencio, 1997). Variation in energy intake among individuals and species can result in a range of energy investment strategies for reproduction (McBride et al., 2013). For instance, floods and droughts can reduce foraging efficiency of drift-feeding fishes, subsequently reducing energy availability for growth and gonad development (Collins and Anderson, 1999; Encina and Granado-Lorencio, 1997). Large fluctuations in flow regimes during extreme hydrologic events can thus lead to delayed maturation and skipped spawning for riverine fishes (Jonsson et al., 2013). While environmental variation may be a strong driver of recruitment, intrinsic drivers such as energy allocation in females may also be equally important in regulating reproductive success.

Here we develop and evaluate a simulation model that assesses ecological impacts of altered flow regimes on *Scaphirhynchus* sturgeon reproductive and recruitment success, and consequences for population sustainability in a regulated river. We use a spatially explicit individual-based population model that explicitly and implicitly simulates individual-level daily activities in response to varying flow regimes (e.g., flow-dependent dispersal, spawning, foraging, and mortality, Fig. 1 and Appendix A in Supplementary material) during the entire life cycle. Further, this model is designed to synthesize currently available information on *Scaphirhynchus* life history (Wildhaber et al., 2007, 2011). Model simulations should shed light on this critical link by examining population-level responses to hydrologic variation that emerge from a variety of individual-level traits. Specifically, we explicitly test the role of energetics as an underlying mechanism of how varying flow regimes drive (1) reproductive ecology including spawning habitat selection and decision to spawn (e.g., spawning frequency and location), and (2) recruitment including settlement location and survival of larvae and juveniles, all of which would ultimately influence population sustainability of fishes in regulated rivers.

2. Methods and materials

2.1. Study species

Scaphirhynchus sturgeon, long-lived iteroparous species with infrequent spawning, rely on repeatability of natural environmental cues such as natural flow dynamics for timing and location of spawning events, and ultimately for recruitment success (DeLonay et al., 2009). Field observations suggest that these river flow-related cues appear to signal these sturgeon for habitat conditions (e.g., water temperature) suitable for spawning and rearing (DeLonay et al., 2009). Yet it is not clear how these observed responses in individual reproductive traits emerge as state dynamics of the populations (Jager, 2001). While recent concerted efforts have gained some insights into the reproductive physiology and behaviors of *Scaphirhynchus* sturgeon in response to altered environmental conditions (Korschgen, 2007), underlying mechanisms of reproduction and recruitment of these species are still poorly identified. There is thus an urgent need to understand the ecological and physiological traits involved in the reproductive and recruitment ecology of *Scaphirhynchus* spp. in regulated rivers to assist sturgeon conservation and river management (DeLonay et al., 2009).

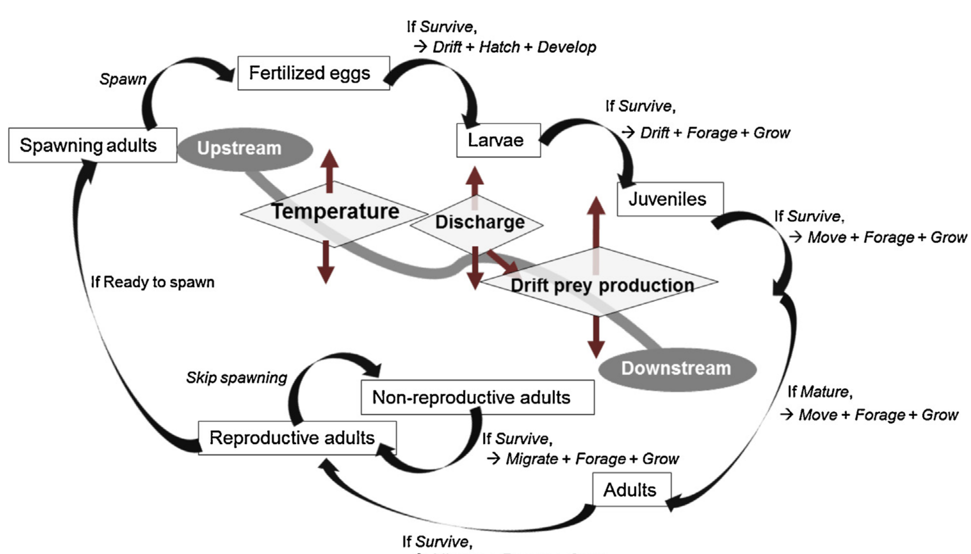

Fig. 1. Conceptual diagram of a spatially explicit individual-based model of shovelnose sturgeon (SEIBM-1D$_{SNS}$). Boxes indicate life stages of shovelnose sturgeon in the model. Italicized texts indicate individual-level processes that facilitate the transition to the next life stage in the model. Diamond shapes indicate environmental drivers (inputs) of the individual-level processes in the model. Detailed description of how the environmental drivers influence each process of the model is provided in Appendix A (Supplementary material).