Ecological Complexity 28 (2016) 1–11

Contents lists available at ScienceDirect

Ecological Complexity

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

Original Research Article

Persistence and diversity of directional landscape connectivity improves biomass pulsing in simulations of expanding and contracting wetlands

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ARTICLE INFO

Article history:
Received 6 May 2016
Received in revised form 22 August 2016
Accepted 24 August 2016
Available online xxx

Keywords:
Flood-pulse
Seasonal hydrology
Dynamic landscape connectivity
Fish movement behavior
Landscape anisotropy
Prediction

ABSTRACT

In flood-pulsed ecosystems, hydrology and landscape structure mediate transfers of energy up the food chain by expanding and contracting in area, enabling spatial expansion and growth of fish populations during rising water levels, and subsequent concentration during the drying phase. Connectivity of flooded areas is dynamic as waters rise and fall, and is largely determined by landscape geomorphology and anisotropy. We developed a methodology for simulating fish dispersal and concentration on spatially-explicit, dynamic floodplain wetlands with pulsed food web dynamics, to evaluate how changes in connectivity through time contribute to the concentration of fish biomass that is essential for higher trophic levels. The model also tracks a connectivity index (DCI) over different compass directions to see if fish biomass dynamics can be related in a simple way to topographic pattern. We demonstrate the model for a seasonally flood-pulsed, oligotrophic system, the Everglades, where flow regimes have been greatly altered. Three dispersing populations of functional fish groups were simulated with empirically-based dispersal rules on two landscapes, and two twelve-year time series of managed water levels for those areas were applied. The topographies of the simulations represented intact and degraded ridge-and-slough landscapes (RSL). Simulation results showed large pulses of biomass concentration forming during the onset of the drying phase, when water levels were falling and fish began to converge into the sloughs. As water levels fell below the ridges, DCI declined over different directions, closing down dispersal lanes, and fish density spiked. Persistence of intermediate levels of connectivity on the intact RSL enabled persistent concentration events throughout the drying phase. The intact landscape also buffered effects of wet season population growth. Water level reversals on both landscapes negatively affected fish densities by depleting fish populations without allowing enough time for them to regenerate. Testable, spatiotemporal predictions of the timing, location, duration, and magnitude of fish concentration pulses were produced by the model, and can be applied to restoration planning.

1. Introduction

Pulsed hydrologic flows play important roles in many aquatic ecosystems by creating conditions for pulses of resource production to form (e.g., fish and invertebrates), which are then concentrated in localized areas (Kahl, 1964; Odum et al., 1995). Concentration occurs over a spatial domain, as these resources are channeled by features of the landscape, at times forming large spikes in density (Yang et al., 2008). Resource pulses may have long-term effects on ecosystems, possibly persisting within and sustaining a system (Holt, 2008; Reigada et al., 2015). It is therefore important to understand how the spatial dynamics of resource pulse concentrations proceed over time.

In seasonally-pulsed wetlands, during the flooding phase, the wetland expands and terrestrial resources are released into the

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http://dx.doi.org/10.1016/j.ecocom.2016.08.004
1476-945X/

aquatic system, boosting primary and secondary biomass production. This biomass then becomes concentrated as waters recede and the wetland dries out and contracts. These ecosystem dynamics occur on river floodplains worldwide (Tockner and Stanford, 2002), and have been termed the 'flood pulse concept' for such systems (Junk et al., 1989; Tockner et al., 2000). This concept is also potentially relevant for other hydrologically pulsed wetlands that are not associated with rivers, or are isolated from them (Tiner, 2003).

Many species of motile biota have adaptive strategies of spreading across the landscape during the flooded phase, and of retreating to locate dry season refugia during periods of low water (Lytle and Poff, 2004; Magoulick and Kobza, 2003). Movement strategies vary by species, and differ in the timing and rates of immigration and emigration (Goss et al., 2014), potentially resulting in successional community dynamics (Winemiller, 1996). Monitoring of fish on floodplains has uncovered many details of movement strategy (Cucherousset et al., 2007; Dutterer et al., 2013; Saint-Paul et al., 2000; Zeug and Winemiller, 2008), but further work is required to understand cumulative effects of growth and movement on flood pulse ecology at the ecosystem level, such as on trophic interactions (Chea et al., 2016; Winemiller and Jepsen, 1998).

Connectivity of flooded areas changes throughout the various phases of rising and falling water levels. When the wetland is flooded, connectivity is considered high and populations can disperse in different directions. As the wetland dries out, connectivity decreases and movement becomes restricted, but a sufficient level of connectivity is needed for fish to continue to move towards refugia. These temporal dynamics of connectivity are thought to impact fish movement and assemblages (Burgess et al., 2013; Lasne et al., 2007). One potential outcome, which we hypothesize, is that the overall flux of fish biomass across the landscape decreases as movement becomes restricted in localized areas, and large concentrations of biomass form that are isolated and removed from the population as areas dry out. Consideration of changes in the pattern of connectivity through time can help to understand the mechanisms of how small-bodied fishes (< 8 cm), which are prey to higher trophic levels, are concentrated in short, localized pulses over long periods of the drying season, to maintain the higher trophic levels (Lake, 2011).

Wetland connectivity is determined in large part by landscape geomorphology. Spatial heterogeneity of the landscape along slight elevation gradients can mediate large shifts in connectivity, as water levels rise and fall, because spatial conformation of the wetland changes over time as different flooded areas become connected and disconnected (Mertes et al., 1995; Zeug and Winemiller, 2008). Patterned landscapes, such as braided riverine networks or parallel drainage landscapes, can have complex connectivity, including directionality. For example, in anisotropic landscapes, connectance is strongly directional when the wetland is partially flooded and some of the topography is exposed, but omnidirectional when water levels rise above the landscape (Fig. 1). These landscape effects, resulting in dynamic patterns of connectivity, have been studied primarily with regard to water flows (Larsen et al., 2012), but are relevant as well to motile biota.

Here, we present a general methodology for evaluating how species-specific movement behaviors interact with dynamic hydrology and heterogeneous landscape geomorphology to produce pulsed concentrations of fish. We combine empirically-characterized movement rules for flood-adapted fish with real landscape topographies and hydrologic data in a computer simulation model called FDAL (Fish Dispersal on Aquatic Landscapes). Fish movement is modeled with both directional and probabilistic elements, as short movements on a contiguous lattice that are based on the local environmental conditions where the fish occupy the landscape.

This model was developed to be broadly applicable to floodplain or transient wetland systems where hydrology, landscape geomorphology, fish movement strategies, and food web dynamics can be estimated. The model simulates and tracks dispersal and concentration of fish over spatially-explicit hydroscapes, and simultaneously tracks connectivity of the flooded wetland over different compass directions. The end product of the modeling is a set of two parallel time series: (1) fish biomass, and (2) directional landscape connectivity indices (DCI) defined over different directions for a given subregion of the wetland. These indices represent the likelihood that a population can traverse that area in a given direction. The time series can be compared and used to make testable predictions of the timing, location, duration, and magnitude of fish concentration pulses, given landscape spatial structure and an annual hydrograph. The capability of the model for simulating fish movement fluxes across a landscape, with spatially varying and temporally dynamic hydrology, is demonstrated here by applying it to a seasonally-pulsed subtropical wetland, the Everglades, using hydrologic records, landscape topographies, and rules for fish movement taken from empirical studies.

2. Methods

2.1. Model description

FDAL simulates population growth, dispersal, and concentration of small-bodied fish in units of biomass (g dry weight m^{-2}). It

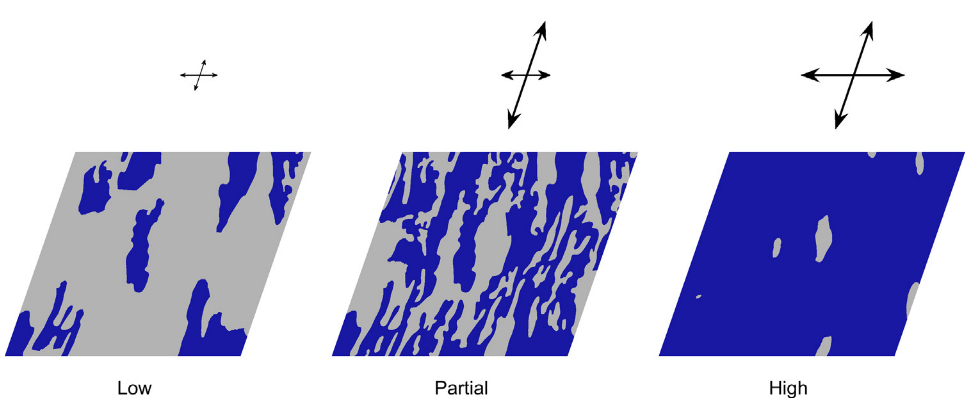

Fig. 1. Dynamic connectivity of a conceptual, anisotropically-patterned landscape over three phases of flooding (blue): low, partial, and high. Gray indicates dry land. Arrow sizes and widths represent relative levels of connectivity over two example directions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)