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Fish population dynamics in a seasonally varying wetland

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ABSTRACT

Small fishes in seasonally flooded environments such as the Everglades are capable of spreading into newly flooded areas and building up substantial biomass. Passive drift cannot account for the rapidity of observed population expansions. To test the 'reaction–diffusion' mechanism for spread of the fish, we estimated their diffusion coefficient and applied a reaction–diffusion model. This mechanism was also too weak to account for the spatial dynamics. Two other hypotheses were tested through modeling. The first—the 'refuge mechanism'—hypothesizes that small remnant populations of small fishes survive the dry season in small permanent bodies of water (refugia), sites where the water level is otherwise below the surface. The second mechanism, which we call the 'dynamic ideal free distribution mechanism' is that consumption by the fish creates a prey density gradient and that fish taxis along this gradient can lead to rapid population expansion in space. We examined the two alternatives and concluded that although refugia may play an important role in recolonization by the fish population during reflooding, only the second, taxis in the direction of the flooding front, seems capable of matching empirical observations. This study has important implications for management of wetlands, as fish biomass is an essential support of higher trophic levels.

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1. Introduction

Many wetland ecosystems are seasonally pulsed; that is, they have distinct wet and dry seasons that cause alternating periods of flooding and drying of large areal expanses (Blum, 1995; Mitsch and Gosselink, 2007). The reflooding of areas that were dry during the preceding season is also the occasion of the expansion of the aquatic food web into those areas (Cucherousset et al., 2007; Rayner et al., 2008; Correa et al., 2008; Mosepele et al., 2009). Exactly how far and how quickly that expansion proceeds is important, because the aquatic food web produces food for higher trophic levels. In the Florida Everglades, USA, for example, small fishes (primarily killifishes (Fundulidae), poeciliids (Poeciliidae), and juvenile sunfishes (Centrarchidae)) are the main food resource of wading birds. Wading birds depend on the seasonal cycle of flooding and drying to produce abundant biomass over a large flooded area during the wet season (Kushlan et al., 1975; Frederick and Spalding, 1994). The small fishes move from permanently flooded wetlands or waterbodies, such as sloughs and canals, into wetlands as they reflood, and their populations and biomass grow in size over the time span of the reflooding. During the dry season, small fish either retreat before the drying front, or become trapped in shallow depressions where they are easily consumed by wading birds and other predators (Loftus and Kushlan, 1987; Gawlik, 2002).

The seasonal expansion of the flooded area in large ecosystems may be substantial, covering hundreds of square kilometers in area, with the 'flooding front' often moving linear distances of greater than 10 km during a flood season. Nonetheless, in the Everglades the small fishes are able to track the flooding front, at movement rates approximating the velocity of the front, and expand in population size to produce much of the new biomass during the wet season that, along with biomass of crayfish, shrimp, and other invertebrates, supports large breeding colonies of wading birds (Trexler et al., 2001; Gawlik, 2002; Russell et al., 2002). Eastern mosquito fish (*Gambusia holbrooki*), flagfish (*Jordanella floridae*), and marsh killifish (*Fundulus confluentus*) are particularly rapid colonizers, with all age classes typically present within days or weeks of marsh reflooding (Loftus and Kushlan, 1987; Trexler et al., 2001; Goss, 2006). While there is some speculation that several species of cyprinodontiform fishes inhabitating the Everglades lay resting eggs that hatch upon rewetting, there is no direct evidence of this (cf. Harrington, 1959; Loftus and Kushlan, 1987). Although resting eggs could con-

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tribute to rapid recolonization upon reflooding, it cannot explain the rapid recolonization by livebearing fishes, such as mosquitofish, or the early reappearance of adult members of most species.

A fundamental question is how a population of small fishes is able to disperse from discrete sources of permanent water, throughout the newly opened area to build up biomass. Three main types of movement are commonly identified for dispersal by animals; passive movement, such as with water currents, random active movements, and directed movements (Armsworth and Roughgarden, 2005). In interior wetlands of the Everglades, water currents are well-below those leading to entrainment of native fishes, seldom exceeding 2 cm s^{-1} (Ho et al., 2009; but see Huang et al., 2008). Entrainment of Everglades fishes would require currents several time stronger than the highest values reported (e.g., Long et al., 1996; Plaut, 2001, 2002; Schaefer, 2001). Furthermore, the direction of flow (roughly from north to south) is perpendicular to the direction of marsh hydration with reflooding (roughly west to east, or east to west, depending on the side of the marsh). Seasonal reflooding occurs by a gradual rise of the water table from below the soil surface to above it, rather than by an influx of current. Therefore, the first of these potential mechanisms, passive dispersal with currents, is assumed to be too small to be considered further.

If passive dispersal is not likely to produce the observed rapid dispersal, then dispersal must involve active movements. A common assumption concerning the spread of an invading species is that the movements of individuals are essentially random, that is, undirected, and that the spread of the population occurs through a combination of population growth and random movements (e.g., Andow et al., 1990). Such a mechanism is embodied in the 'reaction–diffusion model' of Fisher (1937) and Skellam (1951). This assumption has been incorporated in much, probably the proponderant amount, of the theoretical analysis of animal movement (e.g., Okubo, 1980; Williamson, 1996; Czárán, 1998; Shigesada and Kawasaki, 1997; Tilman and Kareiva, 1997; Turchin, 1998; Okubo and Levin, 2001; Cantrell and Cosner, 2003; Malchow et al., 2008). The reaction–diffusion model predicts that invaders can form a 'travelling wave' moving with an invasion speed of $C = 2(aD)^{1/2}$, where a is the intrinsic growth rate of the population and D is the diffusion coefficient.

An alternative mechanism to the reaction–diffusion null model for rapid occupation of a flooded area of fish is that individual fish movement is not random, but biased in the direction of the flooding front. Resources, such as small invertebrates, would be most abundant at the edge of the moving front, because rising water flushes out new resources that have not been exposed to exploitation by fish. In this situation, fish might move preferentially towards higher prey densities, an assumption consistent with the hypothesis that animals tend towards an 'ideal free distribution' (IFD) (Fretwell and Lucas, 1970; Fretwell, 1972), with respect to their resource base. In that case, the velocity of fish invasion is likely to be faster, because some degree of directional movement is present. Armsworth and Roughgarden (2005) noted that this 'directed' movement along an environmental gradient has been relatively neglected by ecological theorists in modeling spatial dispersal. They argue that the more frequent assumption of diffusive movement is likely to apply only in limited cases. A directed movement modeling approach, termed the 'dynamic IFD' hypothesis, has recently been developed mathematically and applied in different contexts (Cosner, 2005; Mari et al., 2008).

It is also possible that rapid dispersal of fish into newly flooded areas is only apparent and is not due primarily to rapid movements. We term this alternative the 'refuge mechanism' hypothesis. According to this mechanism, there are small ponds and solution holes connected to the aquifer (i.e., refugia), which can maintain tiny populations of small fishes across the landscape during the

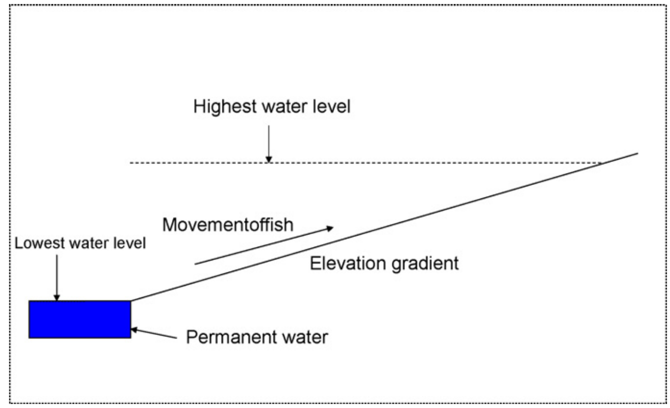

Fig. 1. Elevation gradient simulated by the model. The permanent body of water is assumed to maintain an equilibrium fish population. Water is assumed to rise steadily and flood the marsh during the wet season.

dry season (Loftus et al., 1992). When water levels gradually rise again along an elevation gradient, the small populations in these refugia could provide 'seeds' for population growth as soon as an area is flooded, and small fishes might quickly fill up newly flooded areas. Gaff et al. (2000) noted the possible importance of such refugia for Everglades fishes and Perry and Bond (2009) showed that refugia in an intermittent lowland stream in Australia were vital to long-term persistence of some fish populations, while Chapman et al. (1991) studied the role of refugia in an intermittent stream in Costa Rica.

Our purpose here is to examine these three above hypothesized mechanisms, acting separately or together, for their effectiveness in facilitating the spread and biomass growth of fishes filling the seasonally flooded area to carrying capacity.

2. Methods

We modeled the growth and spread of small fishes on an idealized segment of marsh during the reflooding phase. The spatially explicit model represents the marsh as a tilted plane with a shallow elevational gradient. Water levels alternate between rising and falling through the year, so that a flooding front moves up the plane during the wet season and the drying front moves down the plane during the dry season. It is convenient here to simplify this plane mathematically as having one horizontal dimension that rises in elevation linearly with horizontal distance (Fig. 1). The simulations kept track of water depth at every point on the plane as water levels rise during the wet season. We first estimated a diffusion coefficient for the small fish. This allowed us to test the 'reaction–diffusion' mechanism hypothesis for the spread of the fish population from a single fixed permanent body of water. We then tested the 'refuge mechanism' hypothesis using simulations that supplemented the reaction–diffusion process with an initial uniform distribution of small populations in refugia along the elevation gradient. Finally, we simulated the 'dynamic IFD mechanism' hypothesis that fish create a spatial gradient in resources and follow the flooding front along that gradient.

2.1. Estimation of fish diffusion coefficient

Some estimates the diffusion coefficient, D, for fish populations in the wild are available in the literature. In a field study, mark-recapture of tagged stream fishes provided such diffusion data (Skalski and Gilliam, 2000). After the release of tagged fish at a given stream location, the authors followed and recaptured the fish for 4 months at sites at 11-m intervals along the stream and estimated two coefficients, one for fast fish ($D = 0.4119$ sites^2 day^{-1})