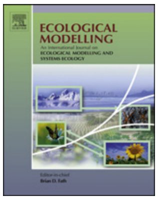
Ecological Modelling 221 (2010) 1131–1137

Contents lists available at ScienceDirect

Ecological Modelling

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



Fish population dynamics in a seasonally varying wetland

Donald L. DeAngelis[a,b,*], Joel C. Trexler[c], Chris Cosner[d], Adam Obaza[c,1], Fred Jopp[b]

[a] *U. S. Geological Survey, Fort Lauderdale, FL 33315, United States*
[b] *Department of Biology, University of Miami, Coral Gables, FL 33124, United States*
[c] *Department of Biology, Florida International University, Miami, FL 33199, United States*
[d] *Department of Mathematics, University of Miami, Coral Gables, FL 33124, United States*

ARTICLE INFO

Article history:
Received 29 June 2009
Received in revised form 5 December 2009
Accepted 21 December 2009
Available online 18 January 2010

Keywords:
Fish functional group
Wetland
Diffusion–reaction model
Ideal free distribution
Fish refugia

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.

Published by Elsevier B.V.

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-

---

* Corresponding author at: Department of Biology, University of Miami, 1301 Memorial Drive, P.O. Box 249118, Coral Gables, FL 33124, United States.
Tel.: +1 305 284 1690; fax: +1 305 284 3039.
E-mail addresses: ddeangelis@bio.miami.edu, don_deangelis@usgs.gov (D.L. DeAngelis).
[1] Present address: IM Systems Group, 501 West Ocean Blvd., Long Beach, CA 90802, United Stated.

0304-3800/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.ecolmodel.2009.12.021

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 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.

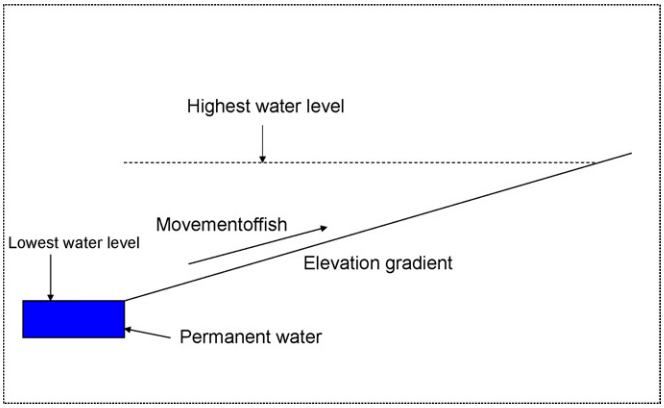


Fig. 1. Elevation gradient simulated by the model. The permanent body of water is assumed to maintain an equilibrium fish population. Water is assumed to rise steadily and flood the marsh during the wet season.

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})

and one for slow fish ($D = 0.0080\ \text{sites}^2\ \text{day}^{-1}$), or, translating the units, $D = 0.005\ \text{km}^2\ \text{day}^{-1}$ and $0.000097\ \text{km}^2\ \text{day}^{-1}$, respectively.

The mark-recapture method was not possible for the small fishes of interest in the Everglades marsh. In principle, however, D can be estimated from microscale data on the random movements of fish; in particular, estimates of the mean time, τ, and the mean distance, λ, a fish moves before turning at some random angle and moving in another direction (e.g., Berg, 1983). Those quantities allow calculation of

$$D = \lambda^2/2\tau. \tag{1}$$

In Obaza et al. (submitted for publication) the mean speed of individual fish, $S = \lambda/\tau$, could be estimated, but neither λ nor τ could be estimated independently. To calculate D, two types of additional information were collected by Obaza et al. First, mean densities of fish numbers, $F_{empirical}$, were measured using a 1 × 1 m throw trap (Jordan et al., 1997). Second, wire-mesh minnow traps were placed at the center of four 12-m drift nets projecting at right angles. The minnow traps formed an 'encounter' sampler trap that collected a percentage of the fish that moved into the vicinity of the trap (details are in Obaza, 2008).

To combine the three types of data (mean fish speed, mean fish density, and rate at which fish are caught in a trap) to determine an estimate of D, we developed a spatially explicit individual-based computer simulation model of fish movement. The model simulated the random movements of many individuals of a model population of fish in the area surrounding and including the drift fences and encounter trap. A sequence of assumed values of λ and τ, each subject to the constraint that their ratio, λ/τ, equalled the mean speed, S, measured by Obaza et al. (submitted for publication), was used in the simulation model to select the pair of values that best matched the rate of capture of fish by the encounter trap, given the measured mean fish density. The specifics of the fish movement model is provided in on line Appendix 1 and in Obaza et al. (submitted for publication).

2.2. Trophic model

For simplicity, the food chain included only fish and their prey, probably mostly small invertebrates. We represented small fish biomass densities by variable $F(s, t)$ and invertebrate biomass by $I(s, t)$, where s is horizontal distance along the elevational gradient, in units of kilometers, and t is time in days. The set of equations describing the dynamics of the predator–prey interaction at any point, s, that is flooded, is, assuming some degree of predator interference in the feeding function (e.g., Beddington, 1975; DeAngelis et al., 1975),

$$\frac{dI(s,t)}{dt} = r\left(1-\frac{I(s,t)}{K}\right)I(s,t) - \frac{fI(s,t)F(s,t)}{1+hfI(s,t)+wfF(s,t)} \tag{2a}$$

$$\frac{dF(s,t)}{dt} = \frac{\gamma fI(s,t)F(s,t)}{1+hfI(s,t)+wfF(s,t)} - mF(s,t), \tag{2b}$$

where r is the growth rate of invertebrates, K is the invertebrate carrying capacity, f is the consumption coefficient, h is prey handling time, γ is the assimilation fraction, w is a predator interference coefficient, and m is the fish mortality rate.

Although we have no direct measurements of most of these parameters, a set of parameters for the predator–prey model was assumed (Table 1), based on reasonable estimates of the maximum rates of growth and carrying capacities of invertebrates and fish. The values of $f = 0.04$, $h = 1.25$, $\gamma = 0.4$, and $m = 0.08$ mean that when the invertebrate prey is at its carrying capacity of $K = 80\ \text{g m}^{-2}$, and when the fish biomass is very small, then the maximum possible daily rate of relative growth of fish biomass is $\gamma fI/(1 + hfI) - m \approx 0.16\ \text{g g}^{-1}\ \text{day}^{-1}$ (see on line Appendix 2). The actual daily rate is generally much less than this because the prey level I is reduced by consumption and because of the fish interference term, wfF, in the denominator. The equilibrium biomasses, calculated using the results of on line Appendix 2, are found to be approximately $I_{equilibrium} = 47.85\ \text{g dW m}^{-2}$ and $F_{equilibrium} = 38.24\ \text{g dW m}^{-2}$.

Table 1
Variables and parameters of Eq. (2a).

Variable	Units	Definition
I	g dry weight m^{-2}	Invertebrates
F	g dry weight m^{-2}	Small fish species populations

Parameter	Value	Units	Definition
r	0.4	day^{-1}	Growth coefficient
K	80.0	g^{-1}	Carrying capacity
f	0.04	g g^{-1} day^{-1}	Consumption coefficient
h	1.25	day g^{-1}	Prey handling time
γ	0.40		Assimilation fraction
m	0.08	day^{-1}	Fish mortality coefficient
w	4.0	day g^{-1}	Predator interference coeff.
v	0.2	km day^{-1}	Flooding front velocity
D		km^2 day^{-1}	Diffusion coefficient
ε		km^2 day^{-1}	Coefficient of attraction to prey

2.3. Modeling fish dynamics, including movement

We simulated one-dimensional movement of the fish in flooded areas of the space, whereas we ignored the spatial movement of the invertebrate populations. We assumed that an invertebrate prey community existed at its carrying capacity prior to the arrival of the fish. This is reasonable, as sedentary invertebrates already exist in the area not yet flooded. The flooding front could be assumed to release nutrients into the water from decomposing plant matter, allowing rapid further build-up of the invertebrate community before the water was deep enough to allow fish to invade. We assumed that the flooding front moved horizontally at a steady velocity, v, to the right in Fig. 1. In the model fish were assumed to invade an area as soon as the water reached adequate depth of a few centimeters.

We used different variations of this basic spatial model to examine the three mechanisms proposed for the spread of the fish.

2.3.1. Case 1. Reaction–diffusion hypothesis

In this case the fish dynamics are assumed to be described by

$$\frac{\partial F(s,t)}{\partial t} = \frac{\gamma fI(s,t)F(s,t)}{1+hfI(s,t)+wfF(s,t)} - mF(s,t) + D\frac{\partial^2 F(s,t)}{\partial s^2}, \tag{3}$$

where the final term is a diffusion term with a constant diffusion coefficient, D, estimated as described above, and the invertebrates are described by Eq. (2a), where invertebrate density, $I(s, t)$, varies with s but does not diffuse. This first model assumes purely random movements of fish, combined with population growth. The source is assumed to be the permanent body of water at the left-hand side of Fig. 1. The equilibrium population density of fishes, $F_{equilibrium}$, in that waterbody forms the boundary condition for Eq. (3), $F(0, t) = F_{equilibrium}$.

2.3.2. Case 2. Refuge mechanism hypothesis

The refuge mechanism hypothesis assumes that during the dry season, small populations of fish survive in refugia such as (in the Everglades, at least) solution holes and alligator ponds scattered across the marsh. To simulate this mechanism, we assumed reaction–diffusion model, but also assumed that for all $s > 0$, $F(s, 0) = F_{refuge} \ll F_{equilibrium}$. In particular, we assumed a series of values $F_{refuge} = \beta F_{equilibrium}$, where β took a series of values from 0.0 to 0.02. The initial conditions for $s > 0$ were not activated until the flooding front reached a point s; that is, when $vt = s$, at which point growth at that point could begin.

2.3.3. Case 3. Dynamic IFD hypothesis

This hypothesis is that the fish follow a gradient of some quantity related to fitness. There is substantial evidence that fish distribute themselves according to IFD, both from experimental laboratory data (Milinski, 1984; Regelmann, 1984; Abrahams, 1989), and from the field (Tyler and Gilliam, 1995). If a mechanism for fish following an IFD is included, then, following Cosner (2005) and Mari et al. (2008), an equation for the fish can be written,

$$\frac{\partial F(s,t)}{\partial t} = \frac{\gamma fI(s,t)F(s,t)}{1+hfI(s,t)+gfF(s,t)} - mF_i(s,t) + D\frac{\partial^2 F(s,t)}{\partial s^2} - \frac{\partial}{\partial s}\left[\varepsilon \frac{\partial G(s,t)}{\partial s}F(s,t)\right], \qquad (4)$$

where $G(s,t)$ is a function measuring the suitability or attractiveness of the habitat, as sensed by the fish. Here we simply chose $G(s,t) = I(s,t)$; that is, the fish were directly attracted by an increasing gradient in invertebrate prey (Liston, 2006). The constant ε represents the strength of the attraction of prey for the fish. A range of assumptions was made for ε. Initial conditions are the same as in Case 1. We also assume that diffusion still occurs.

3. Results

3.1. Diffusion coefficient

From Obaza et al. (submitted for publication), mean fish density, $F_{empirical}$, was found to be roughly10 fish m^{-2}, and the mean fish speed, S, for the fastest of the small fishes was found to by about $S = 0.037$ m s^{-1}, which gives us a value for the ratio $\lambda/\tau = S$. Using this constraint on λ and τ, we performed simulations with different values of λ and τ until agreement was reached with the measured capture rates of the fish. The capture rate of approximately 6 fish per hour agrees with model simulations in which specific values of $\lambda = 0.05$ m and $\tau = 1.25$ s were used. The cumulative captures produced by model simulations for these values agreed well with drift fence empirical results (Obaza et al., submitted for publication), so we used these values to compute $D = 0.001$ m^2 s^{-1}. This converts to $D = 0.000084$ km^2 day^{-1}. This is at best a crude estimate of diffusion but it agrees very closely with the 0.000097 km^2 day^{-1} calculated by Skalski and Gilliam (2000) for slow-moving fish in a stream. This might indicate that our estimate of D is too high, as our estimate is for smaller fish in a more complex environment than studied by Skalski and Gilliam. Nonetheless, we feel it is a reasonable value to use.

3.2. Comparison of models

The 'reaction–diffusion mechanism,' with $D = 0.000084$ km^2 day^{-1} in Eqs. (2a) and (3), resulted in the 1/2-equilibrium point of the fish population reaching only about 0.9 km up the elevation gradient by the time the flooding front had reached a distance of 20 km (Fig. 2a) after 80 days. Note that the traveling wave front of the fish is sharp and reduces the invertebrate prey quickly to their equilibrium values. To examine the effects of other values of D, a range from $D = 0.000005$ to 0.0002 km^2 day^{-1} was then used, and the positions of the 1/2-equilibrium points for each value plotted against D (Fig. 3a).

The 'refuge mechanism' was simulated, in which, in addition to the above reaction–diffusion mechanism, a refuge fish population density of 0.001 (or 0.1%) of the flooded equilibrium fish density was assumed to be distributed uniformly across the landscape initially. This initial population gave a substantial boost to the spread of the fish through the reaction–diffusion equations, with the 1/2-equilibrium position moving up to about 11.4 km (Fig. 2b). Additional results for a range of possible refuge fish population densities, up to 0.025 of the equilibrium biomass, are plotted in Fig. 3b.

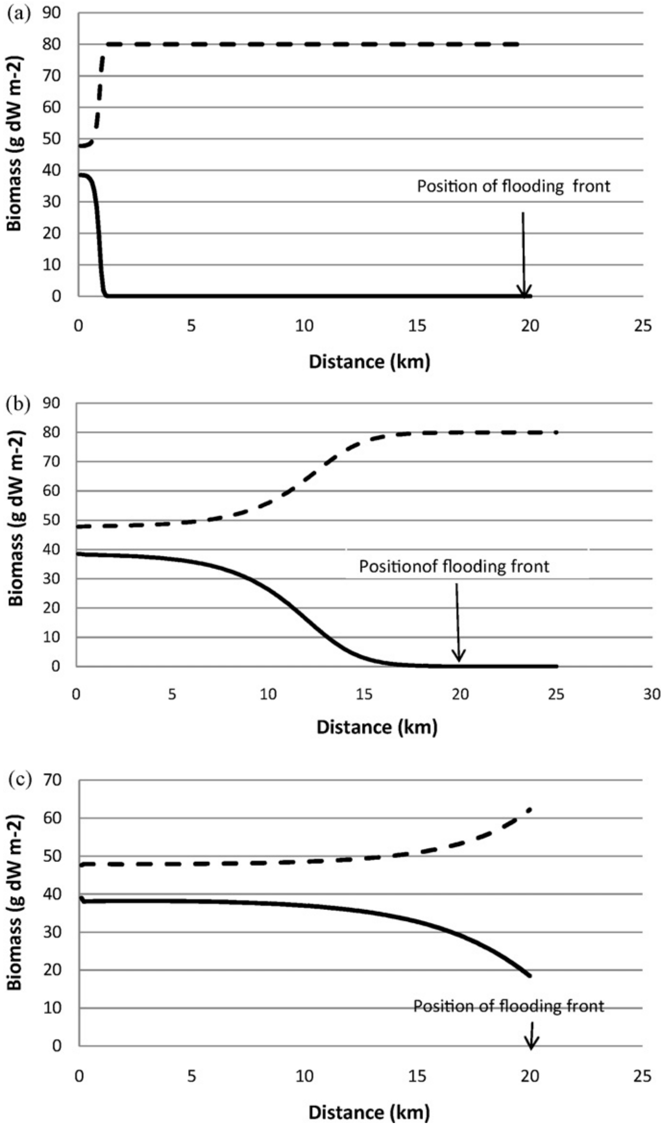


Fig. 2. (a) Distributions of fish (solid line) and invertebrates (dashed line) after 100 days, for the diffusion–reaction model for parameter values of Table 1, for $D = 0.000084$ km^2 day^{-1}. (b) Distributions of fishes and invertebrates after 100 days, with $D = 0.000084$ km^2 day^{-1}, and coupled with an initial refuge fish biomass of $0.001 \times F_{equil} = 0.0382$ g per square meter along the elevation gradient. (c) Distributions fishes and invertebrates after 100 days, from the 'dynamics IFD' model, with an attraction coefficient $\varepsilon = 1.5$. All biomass units are g dW m^{-2}. In each case, the flooding front has reached 20 km at 100 days of rising water.

The 'dynamic IFD mechanism,' which assumed that fish move towards higher prey concentrations and thus following the flooding front, was used with diffusive movement also occurring, with $D = 0.000084$. The results for a particular value of the attraction coefficient, $\varepsilon = 1.5$ km^2 day^{-1}, with the 1/2-equilibrium position of fish biomass at about 20.0 km, are shown in Fig. 2c. Values of ε spanning the range from $\varepsilon = 0.1$ to 2.5 km^2 day^{-1} were then used, and the positions of the 1/2-equilibrium points of the fish for each value plotted against ε (Fig. 3c).

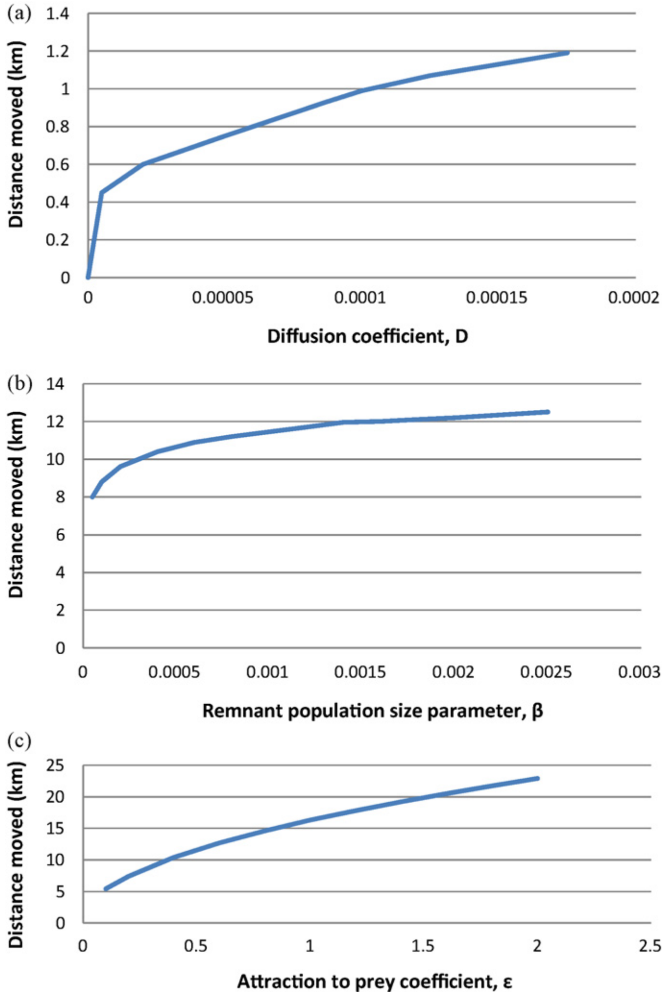


Fig. 3. (a) Number of kilometers reached by the 1/2-height of the travelling wave of fishes as a function of the assumed diffusion coefficient, D, in units of $\text{km}^2\ \text{day}^{-1}$. (b) Number of kilometers reached by the 1/2-height of the travelling wave of fish as a function of the initial sizes of refuge populations in units of fraction, β, of the equilibrium fish biomass under flooded conditions. (c) Number of kilometers reached by the 1/2-height of the travelling wave of fish as a function of the assumed attraction coefficient, ε.

4. Discussion

Large seasonal fluctuations in water level are a feature of many wetlands, including some of the most productive ones (Mitsch and Gosselink, 2007). Seasonal fluctuation of water level in the Everglades, for example, allows expansion of small fishes over an extensive flooded area during the wet season. Surviving small fishes then tend to be concentrated in smaller waterbodies when water levels fall during the dry season, so that fish biomass is available to higher trophic levels, such as wading birds (Loftus and Kushlan, 1987; Trexler et al., 2001). The amount of fish biomass created during the wet season depends on how quickly the populations of small fishes can expand and grow via reproduction. The two key factors governing this are the fish functional group's intrinsic rate of growth and the velocity of movement into the newly flooded areas.

We first argued that passive transport of small fishes into newly flooded areas does not seem to be the mechanism at work in the Everglades, though it certainly may be the case in other systems in which flooding is accompanied by water currents. In the Everglades, reflooding of the marsh is due to a gradual rise in the water table from below- to aboveground. This leaves active movement of the fish as the possible mechanisms of spread. To test the effectiveness of diffusion, coupled with population growth, at producing the size and distribution of biomass of small Everglades fishes, we estimated the diffusion coefficient, based on field data and a model of fish microscale movement. We feel that our estimate of D is more likely to err in being too large than too small, as we used a value of mean fish speed, $S = 0.037\ \text{m}\ \text{s}^{-1}$, at the high end of the estimates made by Obaza et al. (submitted for publication). We used this in a reaction–diffusion model with a fish population growth rate estimate that also might be higher than actual values. The reaction–diffusion model produced a spatial spread of the fish population that is far smaller than that observed. It is not too surprising that the reaction–diffusion model failed to match field observations. This model, which has been applied to a number of species, often tends to predict too slow an advance, as noted by Williamson (1996, p. 99) and Turchin (1998, p. 197). This led us to two possible alternative hypotheses regarding fish movement, which are not mutually exclusive.

The first alternative hypothesis, the 'refuge mechanism' hypothesis is that remnant populations of fishes exist along the elevational gradient, which start to grow and diffuse as soon as the flooding front reaches them. Our simulations indicated that if the mean density in these refuge populations (averaged over the whole area) is about 0.001 of the equilibrium fish population size, their contribution may be substantially more important than that coming from a large permanent source of fish at the lower end of the elevation gradient. This value for residual population allowed the fish population to move around 11 km over 100 days (Fig. 2b), indicating that it is a potential explanation for rapid spatial expansion of the population. However, when the of remant population size is increased much further, to values that are probably unrealistically high, the increase in spatial distance moved is not that much greater (Fig. 3b), so it still does not match the observed rate of spatial expansion. In the Everglades, small bodies of water, such as solution holes in the limestone rock and alligator ponds, may preserve fish in areas where the water level has fallen below ground level. While the sizes of such refuge populations are difficult to estimate, it is doubtful that they are close to the value of 0.0025 or even 0.001 of the equilibrium fish population size, as assumed in these simulations. Therefore, we doubt that feasible values of densities of fish in refugia can facilitate the empirically observed recolonization rates, though it is possible that large numbers of small fishes persist during the dry season in underground solution holes that are hard to detect. In any case, the result does suggest that a possible management strategy for helping to build fish populations during the wet season would be to maintain small permanent waterbodies that can maintain some fishes even during a drydown of water levels. These would certainly help supplement reinvasion from large permanent bodies of water. The role of dry-season refuges in seasonal wetlands may be analogous to climate refuges that have been proposed for post-Pleistocene migration of temperate flora from southern to northern Europe. The spread of species was in some cases faster than reaction–diffusion models are able to duplicate through simulations. This has led to the suggestion that cryptic refugia harbored small populations, which then supplemented the migration as conditions became warmer (Stewart and Lister, 2001; Pearson, 2006; Provan and Bennett, 2008). Simulations of the type we performed might provide estimates of the plausible contributions of refugia to post-Pleistocene expansion.

The second alternative hypothesis for expansion of the fish, the 'dynamic IFD' hypothesis, is that individual fish show preferential movement in the direction of the flooding front. This is incorporated in the last term of Eq. (4), which represents the rate of change of flux, J_f, of fish as being the product of the fish density, the gradient of the prey density, $I(s, t)$, and an 'attraction factor' ε;

$$J_f = \varepsilon \frac{\partial I(s,t)}{\partial s} F(s,t)$$

The attraction factor can be interpreted as the ability of the fish to distinguish differences in prey density and move preferentially in the direction of higher densities. It is clear that a large net flux in the direction of the flooding front is possible in the model for sufficiently large values of ε, since our model predicts a gradient, $\partial I(s, t)/\partial s$, in prey biomass. There are currently no data that allow ε to be estimated independently; therefore, our conclusion that the 'dynamic IFD mechanism' explains spatial spread of fish is only tentative. This would represent the ability of fish to response to gradients in prey availability. The burden for further corroboration of this hypothesis is on behavioral experiments to show that fish can respond to gradients of prey availability. Experiments such as those of Milinski (1984), Regelmann (1984), and Abrahams (1989), adapted to an Everglades-like environment, might allow estimation of ε.

Our study at least casts doubt on the efficacy of a pure 'reaction–diffusion' mechanism for explaining the observed spread of fish in a wetland, but supports the possibility of a 'dynamic IFD' mechanism driving such phenomena. The type of system we have studied is that of a shallow floodplain with a relatively gentle seasonal rise in water levels. Of course, seasonal dynamics of fish have been studied in many contexts. For example, floodplain wetlands of Western Europe, Australia, South America and Africa sustain important fisheries (Welcomme, 1976; Welcomme and Hagborg, 1977; Junk et al., 2000; Welcomme and Halls, 2001; Rayner et al., 2008). Many of those systems have much more dynamic hydrology than the relatively gentle rise and fall of water in rain-driven wetlands such as the Everglades. However, the general principles of active fish movement along prey gradients modeled here may apply across a broad spectrum of ecosystems.

Acknowledgments

DLD was supported by the U. S. Geological Survey and by the USGS's Greater Everglades Priority Ecosystem funding. JCT was supported by Cooperative Agreement J5284060020 between Everglades National Park and Florida International University, funding provided by the Comprehensive Ecosystem Science Initiative (CESI). CC was supported by NSF Grant DMS-0816068. Aspects of this paper are based upon work supported by the National Science Foundation under Grant No. DBI-0620409 and Grant No. DEB-9910514. FJ was supported by the U. S. Geological Survey.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.12.021.

References

Abrahams, M.V., 1989. Foraging guppies and the ideal free distribution: the influence of information on patch choice. Ethology 82, 116–126.

Andow, D.A., Kareiva, P.M., Levin, S.A., Okubo, A., 1990. Spread of invading organisms. Landscape Ecology 4, 177–188.

Armsworth, P.R., Roughgarden, J.E., 2005. The impact of directed versus random movement on population dynamics and biodiversity patterns. The American Naturalist 165, 449–465.

Beddington, J.R., 1975. Mutual interference between parasites or predators and its effect on searching efficiency. Journal of Animal Ecology 44, 331–340.

Berg, H.C., 1983. Random Walks in Biology. Princeton University Press, Princeton, NJ.

Blum, L.K., 1995. Pulsed ecosystems: a new paradigm? Papers from a symposium dedicated to William Eugene Odum (1942–1991). Estuaries 18, 545–546.

Cantrell, R.S., Cosner, C., 2003. Spatial Ecology via Reaction–Diffusion Equations. Wiley Series in Mathematical and Computational Biology. John Wiley & Sons Ltd, Chichester, England.

Chapman, L.J., Kramer, D.L., Chapman, C.A., 1991. Population dynamics of the fish Poecilia gillii (Poeciliidae) in pools of an intermittent tropical stream. Journal of Animal Ecology 60, 441–453.

Correa, S.B., Crampton, W.G.R., Chapman, L.J., Albert, J.S., 2008. A comparison of flooded forest and floating meadow fish assemblages in an upper Amazon floodplain. Journal of Fish Biology 72, 629–644.

Cosner, C., 2005. A dynamic model for the ideal-free distribution as a partial differential equation. Theoretical Population Biology 67, 101–108.

Cucherousset, J., Carpentier, A., Paillisson, J.-M., 2007. How do fish exploit temporary waters throughout a flooding episode? Fisheries Management and Ecology 14, 269–276.

Czárán, T., 1998. Spatiotemporal Models of Population and Community Dynamics. Chapman & Hall, London, England.

DeAngelis, D.L., Goldstein, R.A., O'Neill, R.V., 1975. A model for trophic interaction. Ecology 56, 881–892.

Fisher, R.A., 1937. The wave of advance of advantageous genes. Annals of Eugenics London 7, 355–369.

Frederick, P., Spalding, M.G., 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. In: Davis, S.M., Ogden, J.C. (Eds.), Everglades. The Ecosystem and Its Restoration. St. Lucie Press, Boca Raton, pp. 659–691.

Fretwell, S.D., 1972. Populations in a Seasonal Environment. Princeton University Press, Princeton, NJ.

Fretwell, S.D., Lucas Jr., H.L., 1970. On territorial behavior and other factors influencing habitat distributions in birds. I. Theoretical development. Acta Biotheoretica 19, 16–36.

Gaff, H., DeAngelis, D.L., Gross, L.J., Salinas, R., Shorrosh, M., 2000. A dynamics landscape model for fish in the Everglades and its application to restoration. Ecological Modelling 127, 33–52.

Gawlik, D.E., 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72, 329–346.

Goss, C.W., 2006. Fish colonization of temporary wetlands in the context of the Everglades landscape. M. S. thesis, Florida International University, Miami, Florida, 45 pp.

Harrington Jr., R.W., 1959. Delayed hatching in stranded eggs of marsh killifish, *Fundulus confluentius*. Ecology 40, 430–437.

Ho, D.T., Engel, V.C., Variano, E.A., Schmieder, P.J., Condon, M.E., 2009. Tracer studies of sheet flow in the Florida Everglades. Geophysical Research Letters 36, L09401.

Huang, Y.H., Saiers, J.E., Harvey, J.W., Noe, G.B., Mylon, S., 2008. Advection, dispersion, and filtration of fine particles within emergent vegetation of the Florida Everglades. Water Resources Research 44, W04408.

Jordan, C.F., Coyne, S., Trexler, J.C., 1997. Sampling fishes in heavily vegetated habitats: the effects of habitat structure on sampling characteristics of the 1-m^2 throw trap. Transactions of the American Fisheries Society 126, 1012–1020.

Junk, W.J., Ohly, J.J., Piedade, M.T.F., Soares, M.G.M., 2000. The Central Amazon Floodplain: Actual Use and Options for Sustainable Management. Backhuys Publishers, Leiden, The Netherlands.

Kushlan, J.A., Ogden, J.C., Higer, A.L., 1975. Relation of Water Level and Fish Availability to Wood Stork Reproduction in the Southern Everglades, Florida. Rep. 75-434, US Geological Survey, Tallahassee, FL.

Liston, S.E., 2006. Interactions between nutrient availability and hydroperiod shape macroinvertebrate communities in Florida Everglades marshes. Hydrobiologia 569, 343–357.

Loftus, W.F., Johnson, R.A., Anderson, G.H., 1992. Ecological impacts of the reduction of groundwater levels in short-hydroperiod marshes of the Everglades. In: Stanford, J.A., Simons, J.J. (Eds.), Proceedings of the First International Conference on Ground Water Ecology. American Water Resources Association, pp. 199–208.

Loftus, W.F., Kushlan, J.A., 1987. Freshwater Fishes of Southern Florida. Bulletin of the Florida State Museum, Biological Sciences 31, 147–344.

Long Jr., J.H., Hale, M.E., Mchenry, M.J., Westneat, M.W., 1996. Functions of fish skin: Flexural stiffness and steady swimming of longnose gar Lepisosteus osseus. Journal of Experimental Biology 199, 2139–2151.

Malchow, H., Petrovskii, S.V., Venturino, E., 2008. Spatiotemporal Patterns in Ecology and Epidemiology. Chapman & Hall/CRC Press, Boca Raton, FL.

Mari, L., Casagrandi, R., Gatto, M., Avgar, T., Nathan, R., 2008. Movement strategies of seed predators as determinants of plant recruitment patterns. The American Naturalist 172, 694–711.

Milinski, M., 1984. Competitive resource sharing: a simulation model. Animal Behavior 32, 233–242.

Mitsch, W.J., Gosselink, J.G., 2007. Wetlands. John Wiley & Sons, Hoboken, NJ.

Mosepele, K., Moyle, P.B., Merron, G.S., Purkey, D.R., Mosepele, B., 2009. Fish, floods, and ecosystem engineers: aquatic conservation in the Okavango Delta, Botswana. Bioscience 59, 53–64.

Obaza, A.K., 2008. Effectiveness of Drift Fences in Modeling Fish-Movement Rates. M. S. thesis, Florida International University.

Obaza, A.K., DeAngelis, D.L., Trexler, J.C., submitted for publication. Using data from an encounter sampler to model fish dispersal.

Okubo, A., 1980. Diffusion and Ecological Problems: Mathematical Models. Springer-Verlag, Berlin, 254 pp.

Okubo, A., Levin, S.A., 2001. Diffusion and Ecological Problems: Modern Perspectives. Springer-Verlag, New York, NY.

Pearson, R.G., 2006. Climate change and the migration capacity of species. Trends in Ecology and Evolution 21, 111–113.

Perry, G.L.W., Bond, N.B., 2009. Spatially explicit modeling of habitat dynamics and fish population persistence in an intermittent lowland stream. Ecological Applications 19, 731–746.

Plaut, I., 2002. Does pregnancy affect swimming performance of female mosquitofish, Gambusia affinis? Functional Ecology 16, 290–295.

Plaut, I., 2001. Critical swimming speed: its ecological relevance. Comparative Biochemistry and Physiology Part A 131, 41–50.

Provan, J., Bennett, K.D., 2008. Phytogeographic insights into cryptic glacial refugia. Trends in Ecology and Evolution 23, 564–571.

Rayner, T.S., Pusey, B.J., Pearson, R.G., 2008. Seasonal flooding, instream habitat structure and fish assemblages in the Mulgrave River, north-east Queensland: towards a new conceptual framework for understanding fish-habitat dynamics in small tropical rivers. Marine and Freshwater Research 59, 97–116.

Regelmann, R., 1984. Competitive resource sharing: a simulation model. Animal Behavior 32, 226–232.

Russell, G.J., Bass, O.L., Pimm, S.L., 2002. The effect of hydrological patterns and breeding-season flooding on the numbers and distribution of wading birds in Everglades National Park. Animal Conservation 5, 185–199.

Schaefer, J., 2001. Rifes as barriers to interpool movement by three cyprinids (Notropis boops, Campostoma anomalum and Cyprinella venusta). Freshwater Biology 46, 379–388.

Shigesada, N., Kawasaki, K., 1997. Biological Invasions: Theory and Practice. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford, England.

Skalski, G.T., Gilliam, J.F., 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. Ecology 81, 1685–1700.

Skellam, J.G., 1951. Random dispersal in theoretical populations. Biometrika 38, 196–218.

Stewart, J.R., Lister, A.M., 2001. Cryptic northern refugia and the origins of the modern biota. Trends in Ecology and Evolution 16, 608–613.

Tilman, D., Kareiva, P., 1997. Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions. Princeton University Press, Princeton, NJ.

Trexler, J.C., Loftus, W.F., Jordan, C.F., Chick, J., Kandl, K.L., McElroy, T.C., Bass, O.L., 2001. Ecological scale and its implications for freshwater fishes in the Florida Everglades. In: Porter, J.W., Porter, K.G. (Eds.), The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook. CRC, Boca Raton, pp. 153–181.

Turchin, P., 1998. Quantitative Analysis of Movement. Measuring and Modeling Population Redistribution in Plants and Animals. Sinauer Associates, Sunderland, MA.

Tyler, J.A., Gilliam, J.F., 1995. Ideal free distributions of stream fish: a model and test with minnows. Ecology 76, 580–592.

Welcomme, R.L., 1976. Some general and theoretical considerations on the fish yield of African rivers. Journal of Fish Biology 8, 351–364.

Welcomme, R.L., Hagborg, D., 1977. Towards a model of a floodplain fish population and its fishery. Environmental Biology of Fishes 2, 1–24.

Welcomme, R.L., Halls, A., 2001. Some considerations of the effects of differences in flood patterns on fish populations. Ecohydrology and Hydrobiology 13, 313–321.

Williamson, M., 1996. Biological Invasions. Chapman and Hall, London.