Landscape Ecol (2010) 25:1041–1054
DOI 10.1007/s10980-010-9478-x

RESEARCH ARTICLE

# Modeling seasonal dynamics of small fish cohorts in fluctuating freshwater marsh landscapes

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Received: 3 May 2009 / Accepted: 5 April 2010 / Published online: 28 April 2010

**Abstract** Small-bodied fishes constitute an important assemblage in many wetlands. In wetlands that dry periodically except for small permanent waterbodies, these fishes are quick to respond to change and can undergo large fluctuations in numbers and biomasses. An important aspect of landscapes that are mixtures of marsh and permanent waterbodies is that high rates of biomass production occur in the marshes during flooding phases, while the permanent waterbodies serve as refuges for many biotic components during the dry phases. The temporal and spatial dynamics of the small fishes are ecologically important, as these fishes provide a crucial food base for higher trophic levels, such as wading birds. We develop a simple model that is analytically tractable, describing the main processes of the spatio-temporal dynamics of a population of small-bodied fish in a seasonal wetland environment, consisting of marsh and permanent waterbodies. The population expands into newly flooded areas during the wet season and contracts during declining water levels in the dry season. If the marsh dries completely during these times (a drydown), the fish need refuge in permanent waterbodies. At least three new and general conclusions arise from the model: (1) there is an optimal rate at which fish should expand into a newly flooding area to maximize population production; (2) there is also a fluctuation amplitude of water level that maximizes fish production, and (3) there is an upper limit on the number of fish that can reach a permanent waterbody during a drydown, no matter how large the marsh surface area is that drains into the waterbody. Because water levels can be manipulated in many wetlands, it is useful to have an understanding of the role of these fluctuations.

**Keywords** Wetlands · Transient and permanent waterbodies · Aquatic food web · Trophic cascades · Water level fluctuations · Wetland management · Maximum biomass production · Everglades

**Electronic supplementary material** The online version of this article (doi:10.1007/s10980-010-9478-x) contains supplementary material, which is available to authorized users.

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## Introduction

Large wetland ecosystems are recognized as being “among the most important ecosystems on the Earth” (Mitsch and Gosselink 2007), but are under threat from water diversion, extraction and pollution. Part of their value comes from the diversity of higher trophic level fauna they support, including many endangered or threatened species. Among the more conspicuous features of large wetlands are large rookeries of wading birds, though floodplain wetlands of South America and Africa also sustain important fisheries (Welcomme 1976; Junk et al. 2000; Welcomme and Halls 2001). Productivity of these higher trophic levels is supported by an underlying food web of small fishes and invertebrates that is sustained during dry phases by access to permanently flooded habitats. Many freshwater marshes show strong seasonality with dry and wet phases, which cause seasonal changes in the relative extent of flooded and non-flooded areas (Mitsch and Gosselink 2007). This natural rhythm of rise and fall of water plays an important role in the productivity of the system and the life cycles of the organisms that the wetlands sustain (Wissinger 1999; Batzer et al. 2006). Many wetlands, however, are subject to human impacts that alter the spatial and temporal patterns of hydrology (NRC 1992; Naiman and Turner 2000). Therefore, it is important to understand both the role of seasonality of hydrology on the biota and how a wetland ecosystem may respond to changes in that seasonality (Welcomme and Hagborg 1977; Kushlan 1987; Snodgrass and Burger 2001). Here we apply modeling to provide a basis for quantitative estimation of the impact of hydrology on a small fish population in a wetland.

The Everglades, U. S. A., is a large contiguous wetland that can serve as a model for hydrologically pulsed ecosystems with extensive wetland or floodplain habitats (Davis and Ogden 1994; Snodgrass and Burger 2001). The assemblage of populations of small-bodied fish of the freshwater marshes of the Everglades is affected by their resource base, largely small invertebrates, and by predators, largely piscivorous fish and wading birds (Ogden 1994; DeAngelis et al. 2005). In a seasonally fluctuating wetland, particularly on a flat landscape such as the Everglades, the effective resource base, which is positively related to flooded landscape area, varies tremendously with changes in water level. By ‘small-bodied fish,’ we follow the terminology of others in referring to fish whose adult size is less that 8 cm (Loftus and Kushlan 1987); see also, Jordan et al. (1997), Chick et al. (1999), and Trexler et al. (2001). During the wet season, the area available for small fishes to invade and exploit increases, while in the dry season the small fishes may be compressed into small areas of permanent and semi-permanent water, where density dependence and predation become important factors in their survival (Rehage and Trexler 2006; Rehage and Loftus 2007). Because of the importance of the yearly biomass production of small fishes, scientists and managers are interested in the factors that affect this production (Ogden et al. 2005; Trexler and Goss 2009). Several key factors can be listed.

1. The magnitude of the water level fluctuations is important because it determines the area of newly flooded landscape, and thus determines ‘new’ habitat for fish to expand into each year (Loftus and Eklund 1994).
2. The magnitude of the water level fluctuations may also be a negative factor, if it is associated with low water levels during parts of the year, because this will temporarily compress the habitat of the fish (Kushlan 1976, 1980; Ruetz et al. 2005; Trexler et al. 2005).
3. The rate at which fish can expand into the newly flooded areas is important, as it determines how fast the fish can exploit the flooded marshes before the water again retreats (DeAngelis et al. 1997; DeAngelis et al. in press).
4. Permanent waterbodies within or adjacent to the marsh can serve as refuges for small fishes when water levels in the marsh are very low. These may range in size from large bodies, such as lakes or canals, to small ponds and tiny solution holes in underlying limestone rock (Loftus et al. 1992; Chick et al. 2004; Kobza et al. 2004).
5. However, these waterbodies, especially large ones, such as canals and large ponds or lakes, may harbor predators, such as piscivorous fishes (Rehage and Trexler 2006). The level of predation in permanent waterbodies can determine the fraction of fish that survive during the dry period, and will thus influence the level of biomass that can be built up during the wet period.
6. If marsh areas are flooded over long periods, some piscivorous fish may be able to occupy those areas and reduce the biomass of small fishes available to species such as wading birds (Kushlan 1987; Howard 1995; Trexler et al. 2005).

Many of these factors are related to water-level variation and, therefore, the basic question can be asked: “What is the influence of the water level variation in a freshwater marsh on a population of small fish?” Because the above factors are to some extent amenable to management manipulation, it is important to know how they affect fish biomass productivity.

Here we study some of these factors. The factor of effects of piscivorous fish is postponed until a later paper, but a modeling framework is developed to study the effects of seasonal water level changes. Because of the continuous water level changes, the fish dynamics are non-equilibrium, which can be complex. Modeling a population on a landscape in which the landscape itself is continually changing is a challenge. By simplifying the situation, however, the problem can be made tractable enough to allow a rough, but useful approximation to the dynamics. To reduce complexity, our approach is to first develop a simple analytic model, requiring relatively little empirical data, which can be analyzed in terms of simple algorithms or equations, and which shows clearly the local processes that are involved in the dynamics of a food web under fluctuating water levels in a heterogeneous landscape. We next use a more complex simulation model to corroborate the general conclusions from the simple model. Our specific aim is to make projections of how water level fluctuations in the marsh affect the production and standing stock biomass of a small fish population throughout the year.

## Modeling: Minimal analytic model illustrating key mechanisms

We apply analytic modeling to describe quantitatively the major components of the dynamics of an aquatic food web of a marshland, where water levels are fluctuating and the model marsh landscape slopes gradually upward in elevation away from a permanent waterbody at its lower end. The permanent waterbody is a refuge for small fishes during a severe drydown.

### *Trophic structure of flooded marsh and permanent waterbody*

We first formulate simple food chain models in both the permanent water (e.g., a large pond or canal) and flooded marsh, and examine their static features. This model is ‘minimal’ in the sense of reducing complexity to a bare minimum. The model divides a flat marshland into two landscape features; Region 1 is a marsh area that is flooded for parts of the year, and Region 2 is a smaller area of permanent water. We represent small fish population biomass densities by variables in each region: $F_1$ for the flooded part of the marsh and $F_2$ for permanent water. The resource biomass base of the fish, assumed to consist of small invertebrates, is represented by biomass densities $I_1$ and $I_2$, respectively, in the two regions. We ignore the piscivory from higher trophic levels, such as wading birds, which tends to be more significant during the dry season and on fish that are stranded in shallow ponds.

The set of equations describing the dynamics of these five variables is shown as Eq. 1a–d in Box 1, and the parameter values are defined in Table 1. Note that some parameter values may differ between the flooded areas of marsh and permanent waterbodies. There may be some two-way diffusional movements of fish between the permanent waters and flooded marsh areas, as represented by the constants, $d_{12}$ and $d_{21}$. However, we will assume this diffusion is small and can be ignored, for reasons explained below. Under those conditions, the steady state solutions for the model variables are given as Eq. 2a–d in Box 1.

### *Components of the dynamics*

The above calculations refer to the steady state case with no fluctuations in water level and in which some part of the marsh (or pond or canal) is permanently flooded. Now consider that water levels undergo periods of rising and falling, as well as static periods of water taking on minimum or maximum values for periods of time. The dynamics of the small fish population under such conditions is examined next.

**Box 1** Equations and steady state solutions of the simple model

$$\frac{dI_1}{dy} = r_1\left(1 - \frac{I_1}{K_1}\right)I_1 - \frac{f_1 I_1 F_1}{1+hf_1 F_1} \quad (1a)$$

$$\frac{dF_1}{dt} = \frac{\gamma f_1 I_1 F_1}{1+hf_1 I_1} - m_p F_1 - d_{12}F_1 + d_{21}F_2 \quad (1b)$$

$$\frac{dI_2}{dt} = r_2\left(1 - \frac{I_2}{K_2}\right)I_2 - \frac{f_2 I_2 F_2}{1+hf_2 I_2} \quad (1c)$$

$$\frac{dF_2}{dt} = \frac{\gamma f_2 I_2 F_2}{1+hf_2 I_2} - m_p F_2 - d_{21}F_2 + d_{12}F_1 \quad (1d)$$

$$I_1^* = \frac{m_p}{\gamma f_1 - h} \quad (2a)$$

$$F_1^* = \frac{r_1}{f_1 I_1^*}\left(1 - \frac{I_1^*}{K_1}\right) \quad (2b)$$

$$I_2^* = \frac{m_p}{\gamma f_2 - h} \quad (2c)$$

$$F_2^* = \frac{r_2}{f_2 I_2^*}\left(1 - \frac{I_2^*}{K_2}\right) \quad (2d)$$

**Table 1** Parameter definitions

| Parameter | Definition |
|---|---|
| $r_1$, $r_2$ | Intrinsic growth rate of invertebrates in Regions 1 and 2 |
| $K_1$, $K_2$ | Carrying capacity of invertebrates in Regions 1 and 2 |
| $f_1$ | Consumption rate coefficient of small fishes |
| $f_2$ | Consumption rate coefficient of piscivorous fish |
| $m_p$ | Mortality rate coefficient of small fishes |
| $d_{ij}$ | Transfer rate of small fishes between Regions i and j. |
| $\gamma$ | Assimilation coefficient |

1. To describe the annual cycle, one can start with the expansion of the population as the water levels increase from their minimum values, in which only permanent waterbodies remain flooded, up to a maximum extent of flooding. Simultaneously with the increase in water level to a few centimeters, the small fish follow the expanding flooding front, and grow in population size.
2. A second component may be a period of time over which the water level stays relatively constant at a high level, and during which the small fish population may continue to grow or remain at a constant level if it has reached its carrying capacity, $F_1$* (Eq. 2b).
3. The third component of the dynamics occurs when the water levels recede. Fish that are able to escape will stay ahead of the retreating water front, moving towards lower elevations, thus concentrating in the remaining flooded areas of the marsh.
4. The fourth component of the dynamics occurs when the water level reaches its minimum. If the marsh dries entirely, forcing small fish into the permanent waterbody, the small fish will reach the equilibrium value of $F_2$* (Eq. 2d).

### *Expansion of fish population as water level rises*

A common approach to modeling invasion by a population is to use the reaction–diffusion model of Fisher (1937) and Skellam (1951). This model predicts that the invaders 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. As a first guess, one might imagine that the annual, invasion by fish of newly flooded landscape follows the same mechanism. Because studies of such annual movement in the Everglades show that small fishes appear to follow the invasion front fairly closely, the velocity of movement of the fish predicted by theory should be as high as the velocity of the moving flooding front (Loftus and Kushlan 1987; Trexler et al. 2001; Goss 2006; DeAngelis et al. in press). Generally, such empirical information on diffusion is not available for organisms of real floodplains, although there are some exceptions (for water snails of northern German floodplains, see Jopp 2006). There is no precise information on this value for Everglades fish, but an estimate has recently been made (Obaza 2009). This estimate combined several types of measurements of fish in the field, which resulted in an estimate of the diffusion coefficient of $D = 0.001\ \text{m}^2\ \text{s}^{-1}$, which converts to $D = 0.000084\ \text{km}^2\ \text{day}^{-1}$. This is at best a crude estimate of diffusion, but it agrees very closely with the $0.000097\ \text{km}^2\ \text{day}^{-1}$ calculated by Skalski and Gilliam (2000) for slow-moving fish in a stream. The small fish that we are studying in the Everglades probably diffuse no faster than the slow-moving fish of Skalski and Gilliam, as the Everglades marsh is a much more complex environment. When our estimated value of $D$ is put into a reaction–diffusion partial differential equation model, with a generous estimate of fish population growth, the ½-height point of the advancing fish biomass wave reached only about 0.9 km up the elevation gradient after a 100-day simulation, and very few simulated fish were farther than 1.5 km from the source of fish. Compared with observations that fish populations reach apparent carrying capacities many kilometers from a source of fish within 100 days, we conclude that diffusion alone is too small to account for the movement.

The fish are also unlikely to be carried into newly flooded areas by water currents, as the 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, passive dispersal with currents is assumed to be too small to be considered further. As a consequence, we assume here that the fish follow the flooding front more actively, rather than advancing through either passive drift or diffusive movement. This requires a mechanism for directing movement in the direction of the front. A possible mechanism is that prey availability is higher at the edge of the moving front than behind it, because the rising water flushes up new resources that have not yet been exposed to exploitation by fish. Our assumption is that at each instant a large fraction of fish that are near the front actively follow the front, while the remaining fraction stay behind to feed on the resources in the already flooded areas. Thus we assume the velocity of fish invasion is governed by the rate of physical spread of water that is deep enough for small fish. This hypothesis, like the reaction–diffusion hypothesis, still requires empirical support. For simplicity, invertebrates are not assumed to move spatially, but to grow in population size as soon as an area is flooded. Fish invade later, when the water depth reaches a few centimeters.

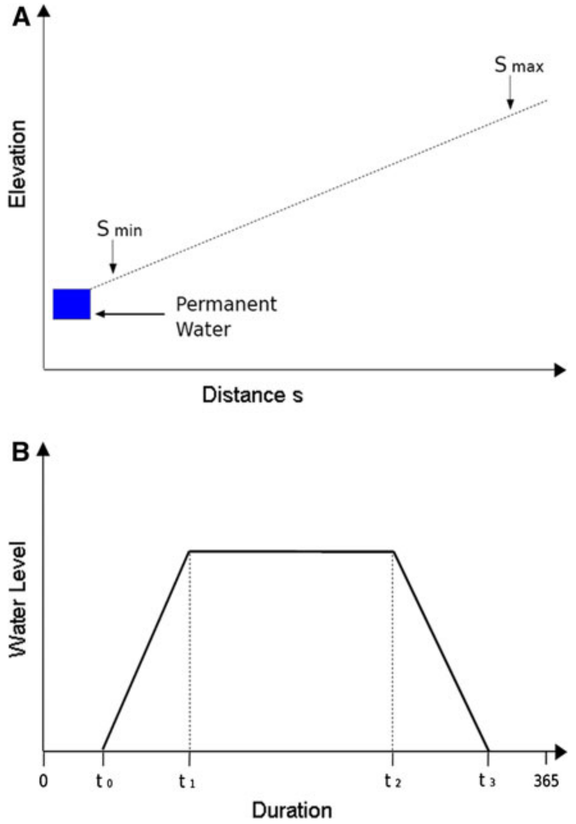


**Fig. 1** **a** Schematic of the landscape, showing a permanent waterbody and an adjacent marsh with gradually increasing elevation. The vertical scale is highly exaggerated. Parameters $s_{\min}$ and $s_{\max}$ represent the water level at its minimum and at its maximum, respectively, for one season. **b** A hypothetical representation of the shape of water levels during the course of a year, measured relative to a point in space where water level was initially precisely zero. The linearity is an idealization. The equations of this paper apply to non-uniform changes

We assume the water rises (between times $t_0$ and $t_1$ in Fig. 1b) and some fraction, *Inv* ($0 < Inv < 1$), of the fish at the flooding front at each instant continue to follow into newly flooded areas; thus, a fraction *1-Inv* remain behind at each instant. Also, the fish population in any area that is flooded and has already been invaded grows, according to equations 1a-b above. For simplicity here, we do not follow the detailed dynamics of the interaction of the fishes with their resources, but merely assume that the fish grow exponentially at a rate $a = \gamma f_1 I_1^{\bullet}/(1 + hf_1 I_1^{\bullet})\text{-}m_f$, where $I_1^{\bullet}$ is the equilibrium resource biomass in the marsh in the absence of fish, $I_1^{\bullet} = K_1$, until reaching a maximum density, $F_1{*} = (r_1/(f_1\ I_1{*}))(1 - I_1\ {*}/K_1)$ (see Eq. 2b). The basic idea behind this simple model is that one does not need information on many parameters, but can estimate the dynamics from a minimal set of parameters; growth rate, $a$, carrying capacity, $F_1{*}$, and fraction of fish at the flooding front that follow the front at each instant rather than remaining in place, *Inv*. The combination of growth and expansion may eventually fill up some of the area to its carrying capacity, depending on the magnitude of $a$ and the length of time that it is flooded. In on-line Appendix 1 this conceptualization is quantified for variable water velocity, so that the density of fish can be estimated at any point of the continuous variable for distance, $s$, along the elevation gradient (horizontal axis). If the water expands horizontally at a rate $v_{\text{flood}}(t)$, starting from the initial position of the water-dry land boundary, $s_{\min}$, and the value of fish biomass for $s \le s_{\min}$ is initially $F_{1,\text{initial}}$ (which may be the equilibrium density within the permanent waterbody, $F_2{*}$, if the marsh had previously dried out), then at any time $t$, during the rising water, the 'invasion profile' of the density of fish is given at location, $s$, by (see on-line Appendix 1)

$$F_1(s,t) = \min[e^{at}F_{1,\text{initial}},\ F_1^*]\ (s < s_{\min}) \tag{3a}$$

$$F_1(s,t) = \min[e^{at}(1 - Inv)(Inv)^{s-s_{\min}}F_{1,\text{initial}},\ F_1^*] \left( s_{\min}\ s < s_{\min} + \int_0^t dt' v_{\text{flood}}(t') \right) \quad 3(b)$$

$$F_1(s,t) = 0 \left( s_{\min} + \int_0^t dt' v_{\text{flood}}(t') < s \right) \tag{3c}$$

where min[*X*, *Y*] is a switching function with the properties, min[*X*, *Y*] = *X* if $X < Y$ and min[*X*,

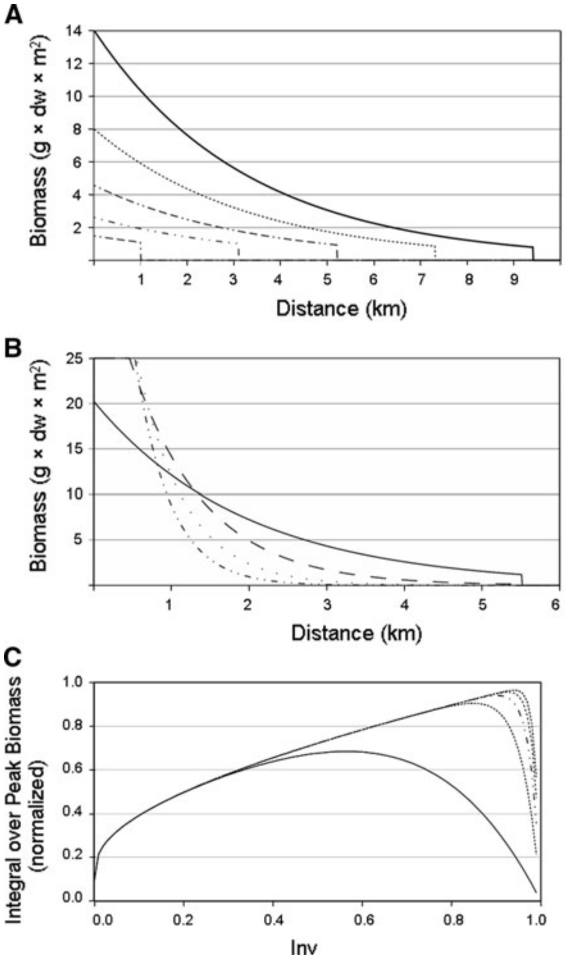


**Fig. 2** **a** Invasion profiles of fish density for five times following the start of the expansion of water in the marsh area. The curves become progressively higher and the front shifts to the right (higher elevation) as time passes. Values of time are 10, 31, 52, 73, and 94 days. The parameter values are $a = 0.04$ day$^{-1}$, $v = 0.1$ km day$^{-1}$, and $Inv = 0.95$. **b** Invasion profiles of fish density for four different values of *Inv* after the same amount of time following the initiation of invasion. The values used are, starting from Series 1, $Inv = 0.95$, 0.90, 0.85, and 0.80. The parameter values are $a = 0.15$ day$^{-1}$, $v = 1.5$, $s_{\min} = 5.0$ km, $t = 40$ days, $F_{1,cc}* = 25$ g wet weight. The curves become increasingly steep at the flooding front as *Inv* approaches 1. **c** Total fish biomass integrated over space (normalized here) as a function of the fraction of fish that advance with the flooding front rather than staying in place. The parameters are $s_{\min} = 0.1$ km, $s_{\max} = 0.5$, 2.5, 4.5, 6.5, 8.5 km

$Y] = Y$ *if* $X \geq Y$ and the position of the flooding front at any time $t$ is given by $s_{\min} + \int dt' v_{\text{flood}}(t')$.

Invasion profiles at different times following the start of flooding are produced by this analytic model (Fig. 2a). The shape and movement of the invasion profile depends on the parameters $a$ and *Inv*, and the velocity, $v_{\text{flood}}(t)$ (set to a constant in the calculations here). The effect of *Inv* is shown in Fig. 2b for five different values of *Inv*, illustrating the sharpening of the profile immediately at the flooding front as *Inv* increases. It can be shown that there is an 'optimal' value of the fraction of fish following the flooding front, *Inv*, which results in a maximum biomass level when the water level reaches its maximum. To show this for the special case in which the fish biomass does not reach its carrying capacity, $F_1*$, at any point along the elevation gradient, we integrate biomass over all space within the range of water level fluctuations ($s_{\min}$ to $s_{\max}$) at the time the water reaches its maximum level, $t_{\text{end}}$, to get the total fish biomass of the system, $F_{\text{total}}(Inv)$:

$$F_{\text{total}}(Inv) = e^{at_{\text{end}}}(1 - Inv)F_{1,\text{initial}} \int_{s_{\min}}^{s_{\max}} ds'(Inv)^{s - s_{\min}}$$

$$= e^{at_{\text{end}}} F_{1,\text{initial}} \left[ \frac{(1 - Inv)(Inv^{(s_{\max} - s_{\min})} - 1)}{\log(Inv)} \right] \tag{4}$$

$F_{\text{total}}(Inv)$ is plotted against *Inv* for five different values of $s_{\max}$ (Fig. 2c) (this in normalized in the figure by dividing by $e^{at}F_{1,\text{initial}}$). Note that there is a peak in each case, indicating that there is a value of *Inv* that leads to maximum biomass integrated over space when the flooding front reaches some level $s_{\max}$ at some time $t$. The larger $s_{\max}$ is, the further the peak is skewed towards larger values of *Inv*. It makes sense intuitively that, the larger the region for fish to expand into, the larger the value of *Inv* that maximizes biomass growth over time. If $F_1(s,t)$ reaches $F_1*$ for some values of $s$ at time $t$, the determination of the value of *Inv* that maximizes $F_{\text{total}}(Inv)$ is slightly more complex, but not more difficult.

### *Stationary period of high water*

If the water level remains stationary for some length of time, as between time $t_1$ and $t_2$ in Fig. 1b, then $v(t) = 0$ and no further area is flooded, but the fish populations at each flooded point along the elevation gradient will continue to grow with increasing $t$, until they reach their limit $F_1*$.

### *Contraction of fish population as water levels recede*

After the water level has risen to its maximum at the end of the wet season, a large area of the landscape may be flooded. We define by $F_{1,\max}(s)$ the distribution of fish biomass along the elevation gradient, where the subscript '*max*' refers to the situation of water level reaching its maximum for the year. As water levels recede, the landscape gradually dries down, starting with highest elevation. Some fraction of fish is able to move ahead of the drying front and escape being stranded. These escapees add to the population of lower elevation areas, which then in turn become dry. The result is a pulse of fish, moving with velocity $v_{\text{dry}}(t)$ toward lower elevations. This is important, as it might serve for wading birds concentrate on these high densities.

We can project the movement of fish ahead of the drying front towards lower elevations and changes in fish densities using an equation applying to continuous time and space, assuming only a fraction of those fish immediately ahead of the drying front move to lower elevations. Taking into account variable drying front velocity, $v_{\text{dry}}(t)$, and the condition that the density of fish not exceed the carrying capacity, $F_1{}^*$, per unit area, except at the location of the pulse, we have, for the density of fish at any time $t$ and spatial point $s$:

$$F_1(s,t) = 0 \quad \left(s > s_{\max} - \int_0^t dt' v_{\text{dry}}(t')\right) \tag{5a}$$

$$F_1(s,t) = \int_{s_{\max}}^{s} ds' (Surv)^{s'-s} \min[e^{at}F_{1,\max}(s), F_1^*] \quad \left(s = s_{\max} - \int_0^t dt' v_{\text{dry}}(t')\right) \tag{5b}$$

$$F_1(s,t) = \min[e^{at}F_{1,\max}(s), F_1^*] \quad \left(s < s_{\max} - \int_0^t dt' v_{\text{dry}}(t')\right), \tag{5c}$$

where *Surv* is the fraction per unit distance of fish that are able to escape being stranded, and min[*X*, *Y*] was defined earlier. The parameter $s_{\max}$ is the position of the maximum elevation that is flooded, time is measured from zero at the start of receding water, and the time integral over $v_{\text{dry}}(t)$ (assumed constant in the model output generated) gives the position of the drying front at any time $t$. In particular, Eq. 5b shows the magnitude of the 'pulse' density of small fish just immediately ahead of the drying front. Figure 3 shows three snapshots of the temporal course of a pulse of fish moving down the elevation gradient during a drydown.

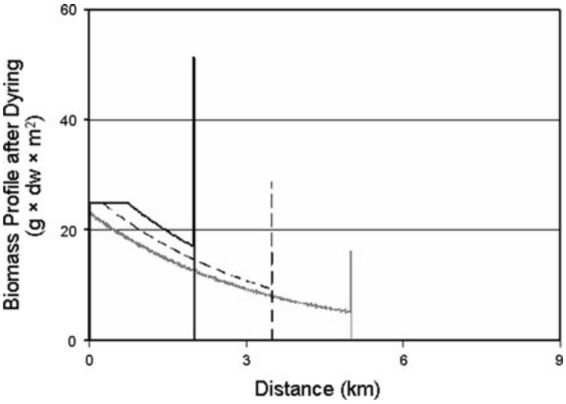


**Fig. 3** Growing pulse of fish retreating from the right towards lower elevations during a single drying period. The fraction of fish escaping each cell is $Surv = 0.70$, while, $a = 0.005$ day$^{-1}$, $v = 0.5$, $s_{\max} = 10.0$ km, and $t = 100$, 130, 160 days from the start of drying

An interesting result can be shown for Eq. 5b. Consider the case in which all values of $F_{1,\max}(s)$ had reached their maximum values of $F_1{}^*$ at the time water levels start to recede. The integral in (5b) can easily be evaluated and shown in the limit $s_{\max} \to \infty$ to be

$$\int_{\infty}^{s} ds'(Surv)^{s'-s}F^*_{1,\text{cc}} = \frac{-F_1^*}{\log(Surv)}. \tag{6}$$

Therefore, there is an upper limit on the height of the pulse of fish moving ahead of the drying front, which is approached asymptotically and is totally determined by *Surv* and $F_1^*$. No matter how long the elevation gradient, or $s$-axis, is, the pulse of fish that eventually reaches the lowest elevation of the drydown cannot exceed a value that is fixed by *Surv* and $F_1{}^*$ (Eq. 6). A similar limitation can be found for any initial fish density profile.

If water recedes only partially down the slope and not all the way to the permanent waterbody, Eq. 5a–c give the final distribution of small fish biomasses at the end of the dry season. If the entire marsh dries out, Eq. 6 determines the amount of biomass, $F_{\mathrm{surv}}$, which escapes into the permanent waterbody.

### *Dynamics of small fishes in permanent waterbody*

It is possible that the fluctuations will lead to an occasional or perhaps periodic drydown of the marsh. In that case, only the small fishes that escape into the permanent waterbody can survive. Recall that biomass of small fishes in the permanent waterbody tends towards, $F_2$*. As a pulse of fish moves into the permanent waterbody to escape a drydown, biomass of small fish in the waterbody increases. Denote this addition as $F_{\mathrm{surv}}$ (= $-F_1$*/*log(surv)* maximum) so that the biomass in the waterbody increases to $F_2^* + F_{\mathrm{surv}}$. The subsequent dynamics in the waterbody are described by Eq. 1c, d. But if the time during which the fish are confined to the permanent waterbody is small, it may not be unreasonable to assume that the population density simply decays exponentially to $F_2$*.

Under these approximations, the Eqs. 3a–c, 5a–c, along with the rule that if the marsh dries out the density of small fishes reaches $F_2$* (Eq. 2b), can be combined to give an estimate of the overall dynamics of the small fish population through the seasonal cycle. These are only approximations for the more complex dynamics that are likely to occur, but they may provide insights into what factors affect the overall dynamics. They also indicate that a relatively small set of values associated with the marsh/waterbody dynamics may be sufficient to make rough predictions concerning the biomass dynamics for a given hydrologic scenario. In particular, we need to know the following:

- fraction of fish per unit distance that follows a flooding front, *Inv*,
- maximum level of fish biomass (carrying capacity) that can be supported per unit marsh area, $F_1$*,
- fraction of fish per unit distance that escapes drying, *Surv*,
- growth rate of the fish population in flooded areas, *a*.

Using reasonable estimates for the parameters, we can combine the expansion of fish during the flooding period, the contraction during the drying period, and the dynamics of small fishes in the permanent waterbody, if they are forced into it, to compute the biomass dynamics of the small fishes through the year. The model can be applied continuously over many years, allowing different patterns of hydrology each year.

### *Effect of water level fluctuations on fish biomass along elevation gradient*

A basic question of a seasonally varying marsh is how the amplitude of seasonal fluctuations in water level affects the biomass of small fishes. This question may be of some practical importance, because in managed wetlands, some control over these seasonal fluctuations is possible. The larger the amplitude of fluctuations, the larger is the area of land that alternates between the flooded and dry states. When an area is flooded in the wet season, it is invaded by the small fish population, which follows the flooding wave. As the water recedes during the dry season, much of this biomass is stranded in shallow water, where it becomes available to foragers like wading birds. Because of this, the dry season is often a prime season for wading bird nesting. A measure of the value of the wetland to wading birds is the amount of small fish biomass created along the elevation gradient by the end of the wet season, because that biomass will become available to wading birds as the water levels go down.

The amplitude of the fluctuations may have an effect on total fish production. Consider a schematic showing a portion of elevational slope of a wetland (Fig. 4a). Suppose there is a regular pattern of seasonal fluctuations of water level between the points $s_{1,\min}$ and $s_{1,\max}$. Recall that at the end of the wet season, this produces the distribution of biomass along the elevation gradient given by Eq. (3a–c). Then the total amount of biomass between $s_{1,\min}$ and $s_{1,\max}$ at time $t_{\mathrm{end}}$, which we will term the end of the wet season, is, from Eq. 4,

$$F_{\mathrm{total}}(Inv) = F_1^*\left(s_{\mathrm{limit}} - s_{1,\min}\right) + e^{at_{\mathrm{end}}}F_{1,\mathrm{initial}} \left[\frac{(1 - Inv)\left(Inv^{\left(s_{1,\max} - s_{\mathrm{limit}}\right)} - 1\right)}{\log(Inv)}\right], \quad (7)$$

where we designate by $s_{\mathrm{limit}}$ the point along the elevation gradient above which the fish biomass has not reached its carrying capacity, $F_1^*$, and so the

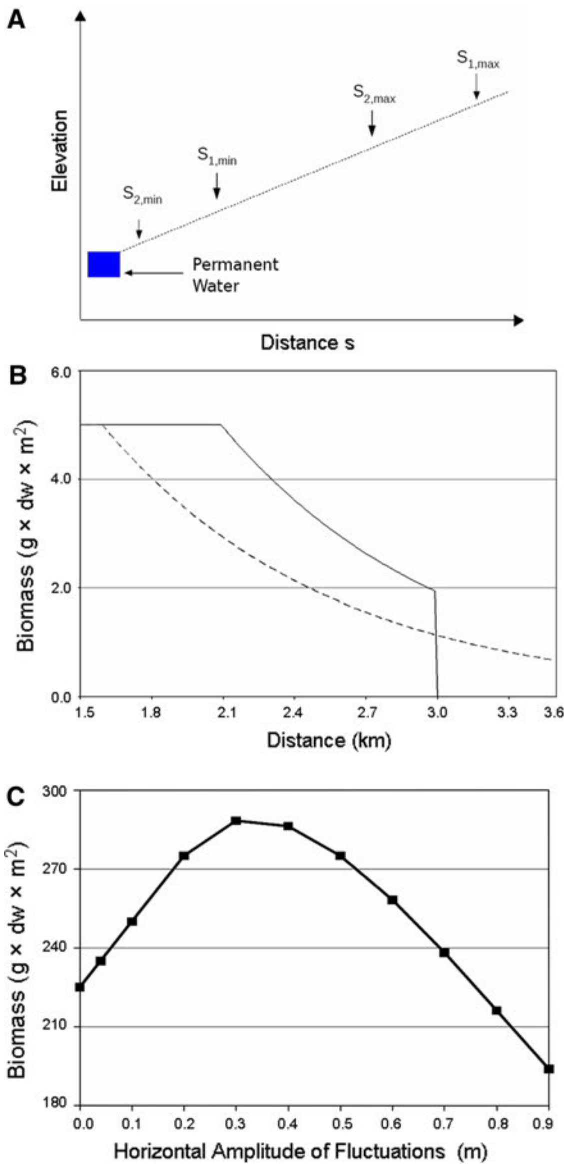


**Fig. 4** **a** Schematic showing two different hypothetical amplitudes of fluctuations between the two points $s_{1,\min} = 2.0$ km and $s_{1,\max} = 3.0$ km (case 1) and between $s_{2,\min} = 1.5$ and $s_{2,\max} = 3.5$ (case 2), respectively. **b** Distribution of fish biomass at the end of the rainy season along the elevation gradient for the two cases of water level fluctuations: Case 1 (*solid line*) $s_{1,\min} = 2.0$ and $s_{1,\max} = 3.0$ Case 2 (*dashed line*) between $s_{2,\min} = 1.5$ and $s_{2,\max} = 3.5$. Parameter values are $Inv = 0.9$, $a = 0.024$ day$^{-1}$, $v = (s_{i,\max} - s_{i,\min})/100.$, $F_{1,\mathrm{cc}}{}^* = 5.0$ g wet weight, $t = 100$. (**c**) Total fish biomasses between points $s_{\max} = 2.0$ and $s_{\min} = 11.0$ (*Note*: this covers a different spatial extent than that shown in b) for fluctuation amplitudes around the mean water level at $s_{\mathrm{mean}} = 6.5$ ranging from 0.0 to 9.0 km distance. Parameter values are $a = 0.04$, $Inv = 0.95$, $F_{1,\mathrm{cc}}{}^* = 5.0$ g wet weight, and v is adjusted to cover the distance between $s_{\min}$ and $s_{\max}$ in 100 days

biomass at elevations above that is still described as increasing in time (see on-line Appendix 1). The first term represents integration over the area of marsh in which fish biomass has reached $F_1^*$ between the points $s_{1,\min}$ and $s_{\mathrm{limit}}$. The second term represents the level that biomass had reached between points $s_{\mathrm{limit}}$ and $s_{1,\max}$ by the end of the wet season.

We examine now what happens if the amplitude of the water level fluctuations increases such that the upper limit of the flooded zone alternates between $s_{2,\min}$ and $s_{2,\max}$. The question is whether this increase in amplitude increases the amount of biomass at the end of the wet season. The increase in amplitude allows the new segment between $s_{1,\max}$ and $s_{2,\max}$ to be flooded and thus to be able to sustain fish biomass. However, now the segment between $s_{2,\min}$ and $s_{1,\min}$ dries out for part of the year. We assume that the biomass in segment $s_{1,\min}$ and $s_{2,\min}$, in the absence of fluctuating water, so that it is flooded, has the total biomass level, $F_1^*(s_{2,\min} - s_{1,\min})$. The total fish biomass integrated over the elevation gradient from $s_{2,\min}$ to $s_{2,\max}$ at the end of the growing season, for the two cases, is, assuming that other parameters are identical in the two cases:Case 1: Fluctuations between $s_{1,\min}$ and $s_{1,\max}$:

$$F_{1,\mathrm{total}}(Case\ 1) = F_1^*(s_{\mathrm{limit},1} - s_{2,\min}) + e^{at_{\mathrm{end}}} F_{1,\mathrm{initial}} \left[\frac{(1 - Inv)(Inv^{(s_{1,\max} - s_{\mathrm{limit},1})} - 1)}{\log(Inv)}\right] \tag{8a}$$

Case 2: Fluctuations between $s_{2,\min}$ and $s_{2,\max}$:

$$F_{2,\mathrm{total}}(Case\ 2) = F_1^*(s_{\mathrm{limit},2} - s_{2,\min}) + e^{at_{\mathrm{end}}} F_{1,\mathrm{initial}} \left[\frac{(1 - Inv)(Inv^{(s_{2,\max} - s_{\mathrm{limit},2})} - 1)}{\log(Inv)}\right] \tag{8b}$$

where $s_{\mathrm{limit},1}$ and $s_{\mathrm{lmit},2}$ denote the positions along the elevation gradient above which, for the two cases, fish biomass had not reached its carrying capacity,$F_1^*$.

Which of these biomasses is larger depends on the parameters $F_1^*$, $a$, $Inv$, and $t_{\mathrm{end}}$, and the extent of the added range of fluctuations $s_{2,\min}$ and $s_{2,\max}$. An example comparison is shown in Fig. 4b. In this case, the increase in the amplitude causes a decrease in the total biomass along the gradient. However, increases in $a$, $Inv$, or $t_{\mathrm{end}}$ can all reverse that inequality. For another set of parameters and for a series of amplitudes, starting with 0 and ending at 90 units (say 9 km) of horizontal distance, the total biomass across the total expanse of 90 spatial units at the end of the wet season was compared for the whole series (Fig. 4c), showing that a maximum exists for an intermediate amplitude. Larger values of $a$ and smaller values of $F_1$* result in larger amplitudes producing more fish biomass, because they improve the likelihood of the fish population being able to fill up the whole area covered by flooding.

## Model: Simulation model, GEFish1

To test some of the general results of the simple analytic model, it useful to supplement this with a simulation model that makes fewer simplifying assumptions. A slightly more elaborated simulation model, GEFish1, is presented, and tested against the prediction of the analytic model for the value of invasion that produces the maximum biomass as the maximum height of the water level. We use this model only briefly here to test the analytic model's prediction of an intermediate fluctuation amplitude that maximizes fish biomass production at the end of the wet season.

### Differential equations of food web dynamics

The basic food web structure of the model is two populations (invertebrates and small fishes), each representing a trophic level, with equations similar to Eq. 1a–d. However, unlike Eq. 1a–d, the functional responses are not Lotka-Volterra, but Beddington–DeAngelis (Beddington 1975; DeAngelis et al. 1975). This takes into account that the fish are somewhat territorial and thus self-limiting, and helps to stabilize the dynamics of the model. Both populations are assumed to be exclusively aquatic, so they cannot persist in dry cells. Equations and parameters of the model are listed in Table 1 of on-line Appendix 2.

### Movement of organisms

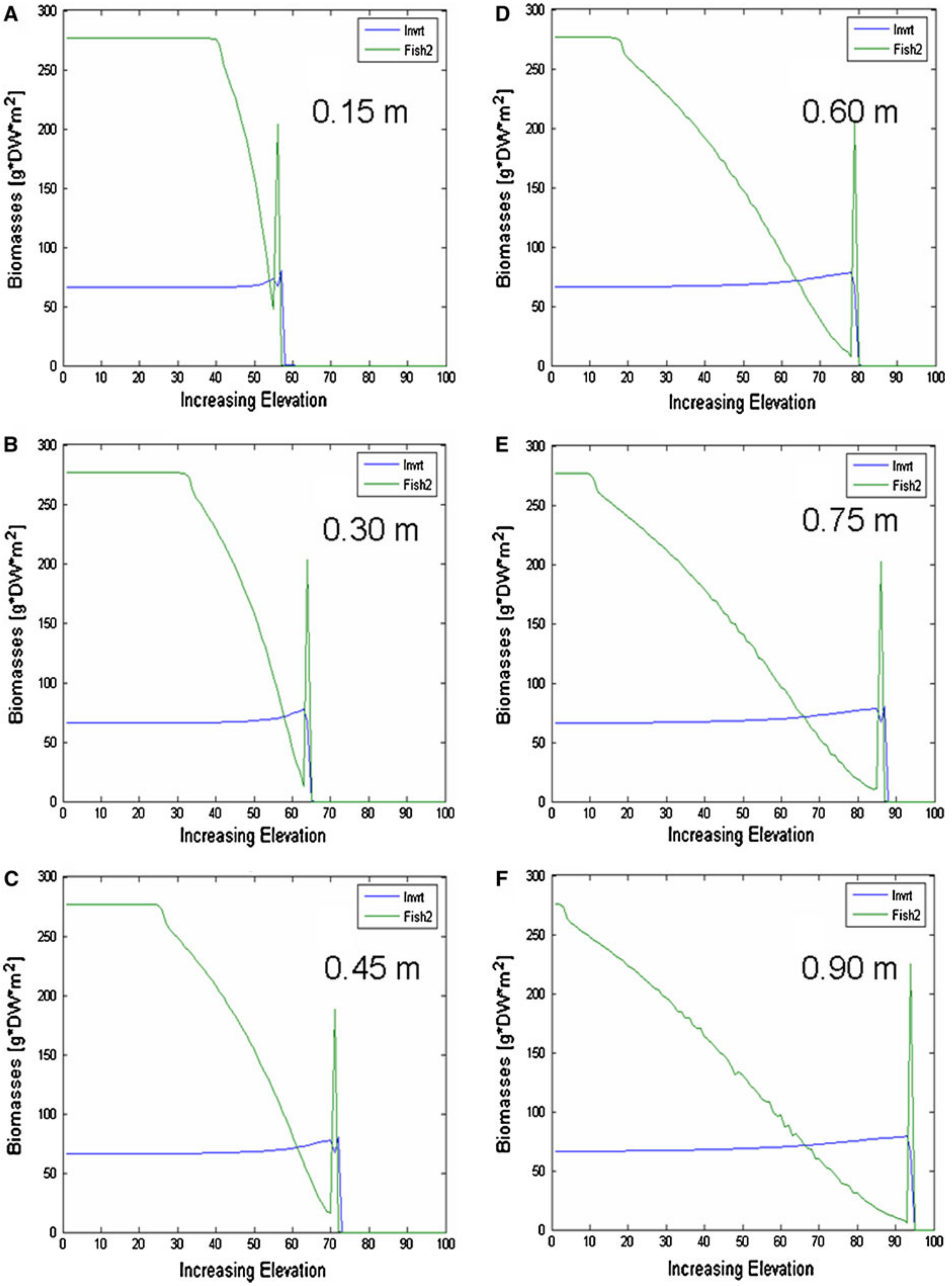
The two main movements of the organisms are the same as in the analytic model; (1) movement out of cells that are drying, and (2) movement into cells that are becoming flooded. The depth threshold for invasion by the fish is 0.01 m, the fractions invading is $Inv = 0.9$ (and the same for leaving a drying cell), and the survival fractions for leaving the drying cell is $Surv = 0.9$.

### Simulations: food web dynamics in the hydroscape at maximum water level for different hydrologic regimes

Our purpose here is only to test the result of the simple analytic model that there exists an intermediate amplitude of seasonal water level fluctuation that maximizes the total fish biomass across the elevation gradient at the end of the period of rising water. We examined the dynamics of the invertebrates and the small fishes on the day the water level reached its highest level and started to recede (day 150 of a given year), assuming sinusoidally varying water levels for six different fluctuation amplitudes along an elevation gradient. These biomass distributions are shown in six snapshots at day 150 in Fig. 5. In these panels, elevation increases to the right, by about 2 m over a 20-km distance, and the sinusoidal water level amplitude about the mean increases in a sequence, beginning at 0.075 m (Fig. 5a) and ending at 0.45 m (Fig. 5f). In no cases did the marsh dry out, so the effect of the permanent waterbody was effectively left out of these simulations.

The most prominent feature in these snapshots are the pulses of the fish and the invertebrates that are shown right at the wave front as the waters begin to recede at day 150 towards the lower elevations of the hydroscape. Also, there are stable fractions of invertebrates and small fishes shown, that reside on the permanently flooded hydroscape on the left side of the panels that are represented as lines parallel to the abscissa (for invertebrates, at about 54 g dW $m^{-2}$, and for small fishes at about 2.62 g dW $m^{-2}$]). Note that the invertebrate population reaches maximum biomass at higher elevations than the fish as they escape the relatively small top–down effect of the fish. The density of small fishes decreases along the

**Fig. 5** Comparison of the food web structure at the day of the onset of water recession water (day 150) in the last year of the simulation (year 5) under different water level regimes. Displayed is the biomass of the invertebrates (*blue*) and the Fish 2 (*green*) versus elevation gradient. The water level vertical (depth) amplitudes are (**a**) 0.15 m, (**b**) 0.30 m, (**c**) 0.45 m, (**d**) 0.60 m, (**e**) 0.75 m, and (**f**) 0.90 m ▶


A
0.15 m
B
0.30 m
C
0.45 m
D
0.60 m
E
0.75 m
F
0.90 m
Invrt
Fish2
Biomasses [g*DW*m^2]
Increasing Elevation
0
50
100
150
200
250
300
0
10
20
30
40
50
60
70
80
90
100

elevation gradient during rising water, representing the limitation on time that the fish have both to move into the newly flooded area and to increase in population size. The pulses of invertebrate and small fish biomass at the flooding front remain more or less unchanged as the water regime changes.

### Biomass production in the hydroscape at receding waters for different hydrologic regimes

We examined the total extant biomass of the invertebrates and the small fishes on the day that water levels started to recede (day 150) under the conditions of changing water level regimes. These connections are given in Fig. 6, where the biomass integrated over the entire transect is shown for different water level amplitudes, ranging from 0.075 to 0.45 m.

It can be seen, that the biomass production of the invertebrates constantly increases with rising water level amplitudes to the right side of the figure. On the other hand, the total biomass of small fishes reaches a maximum (biomass units are arbitrary and so are omitted from Fig. 6) at the low water level amplitude of 0.30 m. After a plateau phase between 0.30 and 0.45 m the biomass production of small fish decreases non-linearly with rising water levels. These results corroborate the theoretical prediction of an amplitude of water fluctuation that is optimal for biomass production.

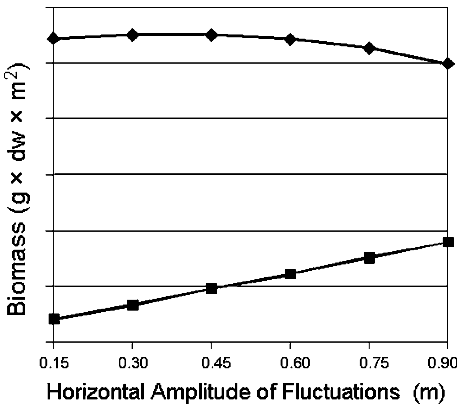


**Fig. 6** Biomass production of invertebrates (*squares*) and fish (*diamonds*) at the day of the onset of water recession (day 150) of the final year of the simulation (year 5) under different water level regimes

## Discussion

The purpose of this work is to provide a rough estimate of seasonal biomass dynamics of a marsh ecosystem with seasonal water level dynamics, and relate the biomass production to the amplitude of water level fluctuations. A simple food chain of invertebrates and small fishes is modeled. This simple food chain may be an important component of energy flow in many marsh ecosystems.

One important result is that reasonable assumptions on fish population growth rate and carrying capacity, combined with an assumption of the fraction of fish moving with the flooding front, are able to produce reasonable patterns of fish biomass along the elevation gradient. Although we do not have time-series empirical biomass information along an elevation gradient to compare with model output, data from sampling in the Everglades indicates that values of 2–5 g wet weight of fish per meter are achieved within a few months of flooding (Loftus and Eklund 1994), consistent with our model results.

From this simple model we also have some important generalizations. Assuming that fish expand actively into newly flooded areas, there is a rate of invasion (fraction of fish that follow the front, *Inv*) that maximizes total fish biomass across the elevation gradient at the end of the period of rising water. Second, there may also be an amplitude of fluctuations that, relative to other amplitudes, maximizes the amount of fish biomass by the end of the period of rising water. Finally, when the water levels recede, the number of fish that ultimately arrive at the remaining wet areas at the end of the drydown depends sensitively on the fraction of fish that stay ahead of the drying front, but not on the area of the drying watershed from which the fish retreat, if the area, measured linearly as $s_{\max}$, is very large.

These conclusions depend on our assumption of active following of both the flooding and drying fronts by the small fishes. Such movement behavior has not been confirmed empirically, but seems to be a more realistic assumption than the exclusively diffusional movement that is commonly assumed in spatial ecological models (Skellam 1951; Okubo 1980; DeAngelis et al. in press). Our computer simulations support these conclusions. We examined here only the analytic result that there exists an amplitude of fluctuations that is optimal for producing total biomass of fish along the elevation gradient. But this conclusion may also have some importance in conservation. As explained earlier, the whole trophic scheme of fishes and invertebrates is within a complex ecological system, with wet and dry phases. In this model, wading birds are implicitly at the end of the aquatic food chain, feeding on fish biomass that remains as water recedes. Wading birds depend on the total fish biomass that exists at the end of the wet season, much of which will be concentrated into small ponds where they are available for consumption (Ogden 1994).

Our model at this stage did not consider the role of piscivorous fish in influencing biomass production and availability of small fishes for wading birds. The addition of canals to marshes and wetlands, yielding a permanent deep-water refuge, could yield dramatic impacts on patterns of water flow and top–down effects of piscivores. The role of canals in Everglades restoration is controversial, because they both provide a productive recreational fishery and elevate the density and diversity of piscivorous fishes that would otherwise be limited by periodic drying of most or all of the marsh. A future application of our model will be to examine the impacts of piscivorous fishes, both those confined to permanent waterbodies and those which can invade the marsh area.

**Acknowledgments** FJ was supported by U. S. Geological Survey's Florida Integrated Science Center, and by the University of Miami, Biology Departement. DLD was supported by the U. S. Geological Survey's Florida Integrated Science Center, 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, and funding provided by the Comprehensive Ecosystem Science Initiative (CESI). Aspects of this paper are based upon work supported by the National Science Foundation under Grant No. DBI-0620409 and Grant No. DEB-9910514. We thank Adam Obaza for comments on earlier versions of this draft.

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