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Modeling fish dynamics and effects of stress in a hydrologically pulsed ecosystem

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Abstract

Many wetlands undergo seasonal cycles in precipitation and water depth. This environmental seasonality is echoed in patterns of production of fish biomass, which, in turn, influence the phenology of other components of the food web, including wading birds. Human activities, such as drainage or other alterations of the hydrology, can exacerbate these natural cycles and result in detrimental stresses on fish production and the higher trophic levels dependent on this production. In this paper we model the seasonal pattern of fish production in a freshwater marsh, with special reference to the Everglades/Big Cypress region of southern Florida. The model illustrates the temporal pattern of production through the year, which can result in very high densities of fish at the end of a hydroperiod (period of flooding), as well as the importance of ponds and other deep depressions, both as refugia and sinks during dry periods. The model predicts that: (1) there is an effective threshold in the length of the hydroperiod that must be exceeded for high fish-population densities to be produced, (2) large, piscivorous fishes do not appear to have a major impact on smaller fishes in the marsh habitat, and (3) the recovery of small-fish populations in the marsh following a major drought may require up to a year. The last of these results is relevant to assessing anthropogenic impacts on marsh production, as these effects may increase the severity and frequency of droughts.

1. Introduction

Fish biomass constitutes a major energy resource for the wading bird communities and other top-level predators of the Everglades and Big Cypress ecosystems of southern Florida. Because this region has distinct wet and dry seasons, the fish communities are exposed to annual fluctuations in water level (Loftus & Kushlan, 1987). The annual drydown concentrates many of the fishes in shallow waterbodies, where they are easily available to predators. Major predators include wintering and breeding wading birds that require high capture rates of prey to feed their nestlings (Ogden, 1994).

Periodic droughts can amplify the effects of the annual dry season and result in the drying of large areas of the Everglades/Big Cypress region. This produces massive losses of fish numbers, and threatens the residual "seed" populations of fishes needed to repopulate the marshes in the next wet season. One of the factors helping to mitigate the severity of the effects of drought are the quasi-permanent waterbodies that exist in many areas, such as creek channels, alligator holes, solution holes, and other depressions, that are refugia for fish during these "drydowns". Fishes that can locate those refuges during drydowns may survive all but the most severe droughts.

These quasi-permanent waterbodies are not guaranteed sanctuaries for fishes that move into them, however. Crowding can lead to oxygen depletion and higher susceptibility to disease. In addition, the larger waterbodies typically house many piscine and reptilian predators. For small fishes, the most significant predators may be the large-bodied fishes, such as Florida gar (*Lepisosteus platyrhincus*), bullhead catfish (*Ictalurus natalis*), and sunfishes (Centrarchidae). Thus, the fraction of small fishes that survive a drydown will be the product of the fraction of fish that move into waterbodies deep enough to last through the drydown and the fraction of those that escape mortality from predation and crowding in these refugia.

These coupled dynamics of water and fishes have continued for thousands of years in southern Florida, with the net result of supporting huge populations of wading birds and their offspring on the annual fish production of the wetlands. Because of human interference, there is now concern about the current functioning of this system of biological energy collection and concentration. Wading bird numbers and reproductive success have declined by an estimated 90% in the southern Everglades (e.g., Fleming et al., 1994). The system of levees and canals built in southern Florida to divert water for urban and agricultural water use and flood control has altered the natural hydrologic cycles over large portions of the Everglades (Fennema et al., 1994), and has reduced the formerly high availabilities of fish for the wading birds over much of this landscape (Fleming et al., 1994; Ogden, 1994). Thus, the system of water regulation has imposed a stress on the natural functioning of the system.

Plans are being made to restore at least some of the natural water flow through the Everglades and Big Cypress ecosystems (e.g., Hinrichson, 1995). But the manner and extent of the restoration have not yet been defined. It is essential that forecasts be made of the expected results for populations of wading birds and other species based on alternative restoration scenarios. A key part of the prediction is how various proposed hydrologic restoration alternatives will affect populations of fishes across the landscape. Each alternative will involve a partial return to natural conditions, but will unavoidably retain much of the present system of dikes and canals.

In this paper we describe a computer simulation model designed to predict the fish population responses to this seasonal pattern of water levels at a particular site (or spatial cell) on the landscape. The model has the following specific objectives. The first is to describe the seasonal dynamics of the community of small fishes [e.g., mosquitofish (*Gambusia holbrooki*) and killifishes (Cyprinodontidae)] as water levels change through the year. These small fishes are major prey items for many wading birds. The second objective is to predict the effects of prolonged droughts on fish populations, which have become more frequent during the past few decades of human intervention. A lengthy period of drought may reduce remnant populations of fish to very low levels, and the recovery of the populations after the drought may be correspondingly slow. The third objective is to examine the potential for large piscivorous fishes to have an appreciable regulatory effect on the smaller fishes that are important to the wading birds. Thus, the piscivorous fishes are modeled as a separate functional type. The model as described here is generic and should apply to freshwater marshes that, like those of the Everglades/Big Cypress region, experience seasonal hydrologic pulses.

The essential dynamics that the model attempts to capture are shown in Figure 1. Figure 1a shows a cross-section of a marsh area under high water, as might occur by the end of an unusually wet rainy season. Both large and small fish swim freely in the marsh, and piscivory will occur there. Figure 1b shows the water level receding, and both large piscivorous fishes (first) and small fishes (later) moving towards whatever deeper water is available. These may be quasi-permanent ponds, shallow depressions, or deeper solution holes that occur in some areas where limestone rock is close to the surface (Loftus et al., 1992). Figure 1c shows the spatial cell largely dried out, with the fishes concentrated into ponds, where intense predation can occur, and in the deep solution holes, where there may not be as much predation from piscivorous fish. Some fishes seeking refuge in shallow depressions are stranded, and may be consumed by wading birds. Figure 1d shows the water level rising again, with the small fish that survived the dry period dispersing into the marsh. The large piscivorous fishes are assumed to disperse into the marsh only if water levels continue to rise.

The computer model attempts to provide a quantitative simulation of the dynamics pictured in Figure 1. The changes in water level are modeled, as are the interactions of the fishes with their resource base of periphyton, macrophytes, mesoinvertebrates, macroinvertebrates, and detritus. The simulation also includes the interaction of large and small fishes to address the question of whether the larger fishes may be a major regulating factor for the small fishes. The description

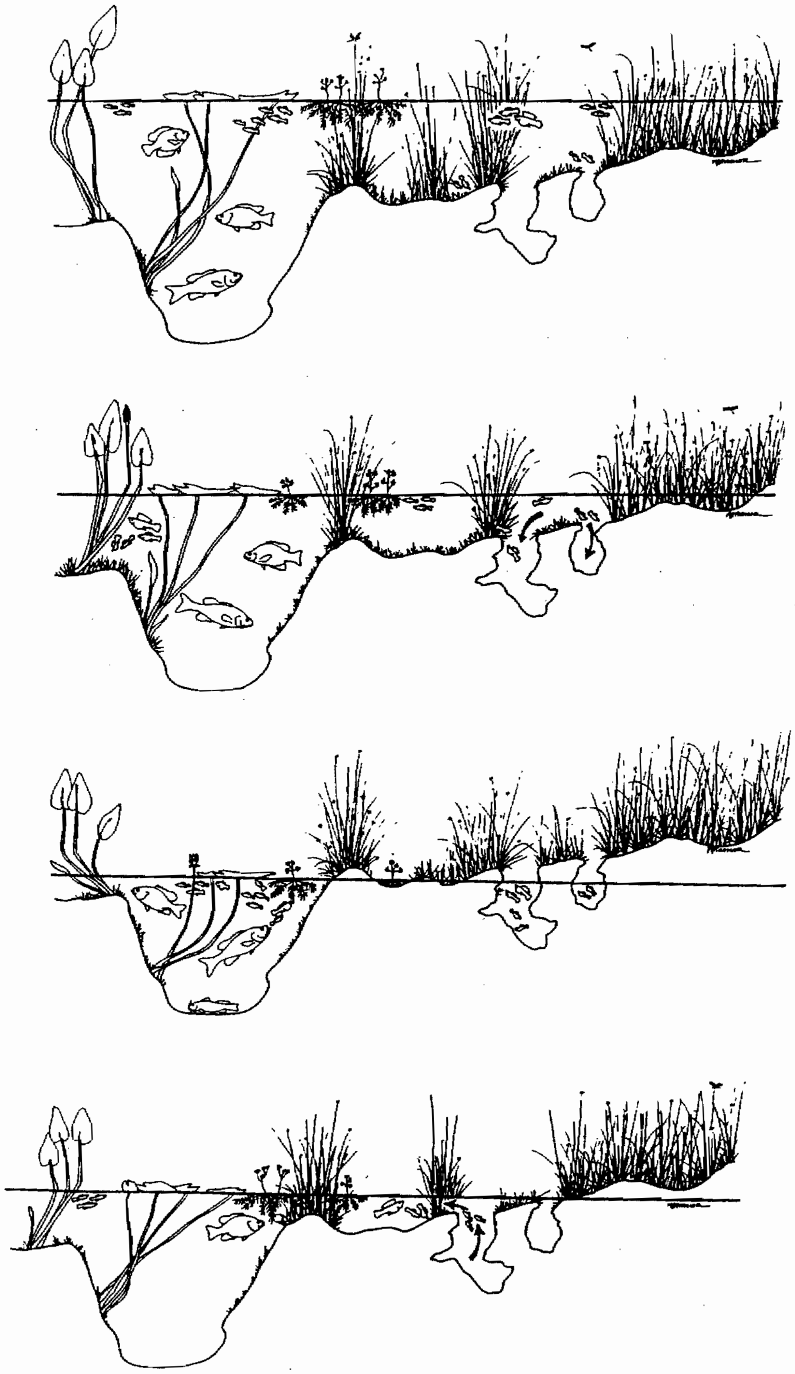

Figure 1. Schematic showing a typical cycle of water levels in an area of Everglades freshwater marsh: (Top) Water levels are high and both small and large fish are present in the flooded marshes. Trophic interactions between these functional groups can occur in the marshes. (Second from top) as water levels recede, large fish and then small fish move into refugia of deeper water. These can include ponds, shallow depressions, and deep depressions (e.g., solution holes). (Third from top) If water levels reach low levels, deep ponds and solution holes may be the only refugia remaining. Intense predation by large fish on small fish may take place in the ponds, but smaller fish may be relatively safe in solution holes, because large fishes may be absent. (Bottom) As water levels rise again, small fish move out from the refugia into the flooded marsh. If water levels become high enough, many large fish may also move into the marsh.

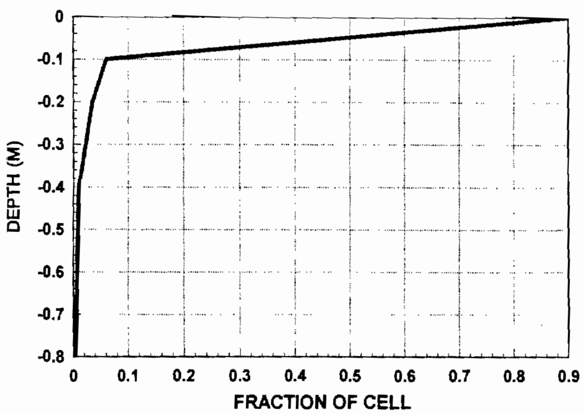

Figure 2. Hypsograph of hypothetical distribution of surface topography of spatial cell. The x-axis is the cumulative area of the cell and the y-axis represents the depth classes of various fractions of this total area.

here is restricted to one spatial cell, but the model is currently being applied to a larger landscape made up of many contiguous spatial cells.

2. Description of model

Physical environment

We chose as our basic landscape unit a spatial cell measuring 500 m × 500 m. This size is somewhat arbitrary, but the idea was to have an area that is small enough to be characterized by a mean elevation, yet large enough that an entire landscape, such as the Everglades/Big Cypress region, could be modeled as a grid of cells. An elevation value was assigned to the cell as a whole, but we assumed the cell was internally heterogeneous with a non-spatially explicit distribution of topographic depressions at elevations below this nominal cell elevation value. In the model, we included the following microtopographic features:

a. A fraction of the cell is occupied by permanent water, a pond.
b. Topographic depressions (including deep erosional features, or solution holes, that occur in some parts of the Everglades) with a spectrum of depths occupying a portion of the cell. These depressions dry out sequentially as the water level drops below the cell surface. Figure 2 is a hypsograph showing the assumed topography of the modeled spatial cell.

The hydrologic condition (water level relative to the cell elevation) of the spatial cell is simulated by

Table 1. Abiotic components of the model

Parameter	Value
Size of spatial cell	250,000 m^2
Size of permanent pond area	50 m^2

Submodel for water depth in the spatial cell through a given year:

$$\text{Water Depth} = \text{Mean Depth} + \text{Amplitude}^{*}\cos\left[2\pi\left(\frac{x - \text{Max Day}}{365}\right)\right]$$

where

Mean Depth = mean depth of water in the cell during the year
Max Day = day of the year on which water depth is a maximum
Amplitude = the amplitude of the water depth cycle

a sinusoidal function within each year (see Table 1, which also specifies other characteristics of the simulated spatial cell). The mean annual water level, MeanDepth, can be specified by the modeler to follow any desired inter-annual trend. The modeler can simulate, for example, the natural alternations of periods of lower than average water levels with years of higher than average water levels. The amount of the permanent pond area, 50 m^2, was selected as not untypical for parts of the Everglades, based on personal observations of the authors.

Lower trophic levels

The ultimate limits on the growth of the fish populations are determined by dynamic models of lower trophic levels (periphyton, macrophytes, mesoinvertebrates, macroinvertebrates, and detritus) that are resources of the fishes. Figure 3 shows the interactions among the lower trophic levels and the feeding relations of the two age-structured fish functional groups. The lower trophic levels are described by process type models for their biomasses. The equations used for the lower trophic levels in this model are shown in Table 2. These equations were based on fits to empirical data from Browder et al. (1981, 1982, 1984) for the Everglades ecosystem. Although the equations in Table 2 show only the relationships among the lower trophic level components, the total model also includes the effects of fishes on the lower trophic level standing stocks.

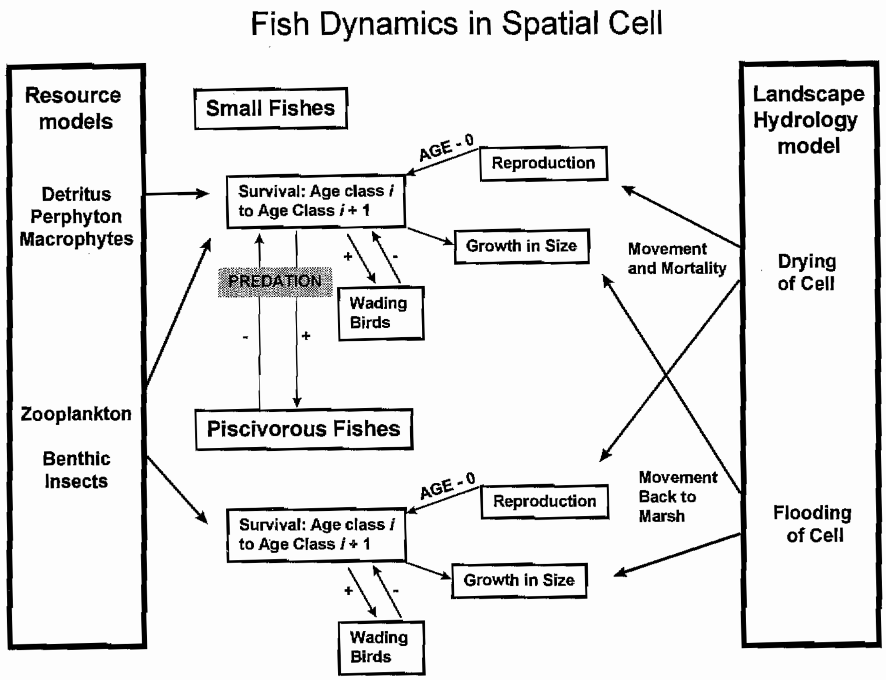

Figure 3. Schematic of the model, which simulates two functional groups of fish, large and small, in the Everglades freshwater marsh. The small fishes and the early age-classes of the large fishes feed on the lower trophic level web. The older age-classes of the large-fish functional type feed almost exclusively on fish of the smaller functional group.

Fish life cycles

Two fish functional types are represented in the model, the "small planktivorous functional type", which includes, for example, *Gambusia* and killifishes and the "large piscivorous functional type" which includes, for example, sunfishes, bullhead catfish, and gar. The fish in each of these two functional types are modeled as 1-month age-classes. Growth in age, growth in size, and mortality occurs on these 5-day time steps, but an increase to the next age-class occurs only on the first time step within a given month. At age s, which is approximately equal to $30 \times i + m_{\text{day}}$ (where i represents the month age-class of a particular fish and m_{day} is the day of the month), the size of the fish (length, L) is calculated from a von Bertalanffy equation:

$$L_i = L_\infty[1 - \mathrm{e}^{K(s-t_0)}],$$

while weight in grams dry weight is given by the weight–length relationship

$$W = \alpha_1 L^{\alpha_2},$$

where L_∞, K, t_0, α_1, and α_2 are constants. The values of these fish growth parameters used in the model are presented in Table 3. Figure 4 shows the growth forms of each functional type. It is assumed that all fish that survive through a given time step grow at the growth rate specified by the von Bertalanffy equation and the weight–length relationship above. We assumed that when the food that could be captured by fish during a particular time step fell below that needed for maintenance, this translated directly into mortality of fish rather than into stunting of growth.

Mature fish of each functional group produce a number of viable offspring during their reproductive season. The age of maturity, the fecundity, and the months during the year in which each functional group reproduces are specified as input data (Table 3).

Three types of mortality assumptions are embodied in the model:

1. Density-independent background mortality, or the natural mortality of an uncrowded population, dependent on fish size class. The age-dependent functional form for the mortality used in this model is shown in Table 4. This mortality is assumed not to include mortality inflicted by the larger functional fish type on the smaller, which is a focal point of this modeling study. Also, large episodic mortality events, such as those caused by large

Table 2. Equations for lower level biomasses. Units of biomass are grams dry weight per square meter

$$\frac{dB_1(t)}{dt} = aB_1(t) - bB_1(t)^2 - c[dB_4(t) + eB_5(t)]B_1(t)$$
$$\frac{dB_2(t)}{dt} = fB_2(t) - gB_2^2(t)$$
$$\frac{dB_3(t)}{dt} = h[bB_1(t)^2 + gB_2(t)^2 + iB_4(t)^2 + jB_5(t)^2] - kB_3(t)$$
$$\frac{dB_4(t)}{dt} = dB_1(t)B_4(t) - iB_4(t)^2$$
$$\frac{dB_5(t)}{dt} = eB_1(t)B_5(t) - jB_5(t)^2$$

where

B_1 = periphyton biomass
B_2 = macrophyte biomass
B_3 = detrital biomass
B_4 = mesoinvertebrate biomass (those <1 mg body weight)
B_5 = macroinvertebrate biomass (those >1 mg body weight)
c = inverse of assimilation rate of macroinvertebrates and mesoinvertebrates

and where the following parameters are seasonally varying:

a = periphyton growth rate
b = periphtyon death rate
f = macrophyte growth rate
g = macrophyte death rate
h = percentage production in detritus
k = detritus decay rate
d = mesoinvertebrate growth rate
i = mesoinvertebrate death rate
e = macroinvertebrate growth parameter
j = macroinvertebrate death rate

flocks of wading birds feeding in a given area, are left of this type of mortality.

2. Density-dependent mortality from starvation. This is calculated by first computing the density of preferred prey for a particular age-class of a particular functional group. As this density of preferred prey decreases, the mortality rate of that specific age-class and functional group increases (see the discussion under Trophic Interactions).
3. Loss due to predation from the other functional group in the model. In particular, fishes of the small functional type are preyed on by the fishes of the large functional type.

These types of mortality are considered as competing risks of mortality, and the actual survivorship of fish of a particular functional type and age through a given time step is calculated by combining those risks.

Table 3. Values of principal life cycle parameters

Parameter	Fish functional type	
	Type 1: Small fish	Type 2: Large fish
von Bertalanffy coefficients:		
L	4.5	45.0
K	−0.015	−0.002
t_0	−6.0	−6.0
Weight–length coefficients:		
α_1	0.00128	0.00128
α_2	3.02	3.02
Age of maturity	30.0	360.0
Fecundity, number of offspring per month, per fish	30.0	20.0
Months in which reproduction occurs	February–November	January–October

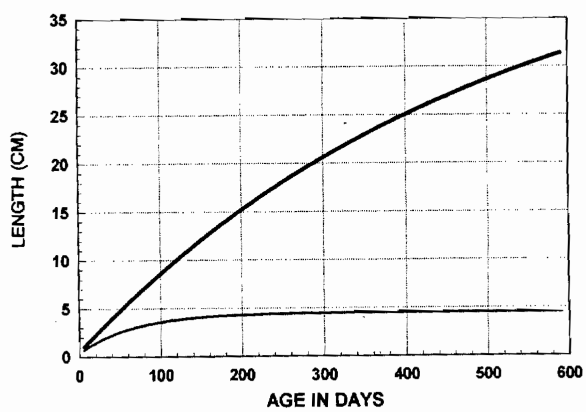

Figure 4. Schematic showing the size versus age in days of fish of the two functional types being modeled. The thicker line represents the growth of the piscivorous fish type, while the thin line represents the small fish type.

Movement patterns

The environmental driving variable is the hydrologic cycle. If and when the water depth in the spatial cell falls to low levels, the fish begin to move to depressions or ponds. The larger fish move first and the smallest fish last. All have moved to depressions before the

Table 4. Density-independent, age-specific mortality. The $p_i s$ are parameters chosen to roughly fit estimated survival curves of the two functional fish groups

The form of the age-specific survival is given by

$$\text{SURVIVAL} = 1.0 - \frac{p_1}{(1.0 + p_2 s)^{p_3}}$$

where s = age of fish in days

Parameter	Fish functional type	
	Type 1: Small fish	Type 2: Large fish
p_1	0.04	0.002
p_2	0.04	0.05
p_3	10.0	10.0

Table 5. Parameters describing movement patterns

Parameter	Functional types	
	Small fish	Large fish
Probability of reaching pond during drydown	0.05	0.20
Probability of reaching depression during drydown	0.20	0.10
Probability of moving from pond to marsh during reflooding	0.9	0.6

depth relative to the surface of the cell falls to zero. Some fraction of the fish present in the spatial cell at each time is allocated either to ponds or to depressions. The fractions of each species that reach ponds or depressions, respectively, can be specified (Table 5). These values shown in Table 5 are only assumptions at present. They are based on observations in the field, but little quantitative evidence exists to support them at present.

As the water level drops further, the portion of a cell area that remains under water diminishes. Only the deeper depressions remain flooded. We assume that the fish can move to the depressions, but that some fraction will reach only shallower, isolated depressions and become stranded as water levels continue to fall. If depressions dry out, or are discovered by wading birds, the fish in them are lost from the population. Those surviving in depressions emerge into the cell when the water level rises again.

Table 6. Parameters describing trophic interactions. Electivity indices representing the fraction of prey of type j that fish funtional group i would take if prey were available in *ad libitum* amounts

Prey	Fish functional type		
	Type 1: Small fish	Type 2: Large fish	
		Year 1	Older
Periphyton	0.3		
Macrophytes			
Detritus			
Mesoinvertebrates	0.5	0.3	
Macroinvertebrates	0.2	0.5	0.5
Fish Functional Type 1		0.2	0.5

Trophic interactions

Figure 3 shows the assumed trophic relationships in this simplified food web. Table 6 shows the electivity indices relating each fish functional type and its prey. These indices imply that, if all potential prey of a functional type are available in unlimited amounts, the functional type would take prey in those proportions. The small-fish functional type is assumed to feed only on lower trophic-level materials, whereas the large-fish functional type undergoes an ontogenetic shift from small prey (taken from lower trophic levels) to fish of the small-fish functional type.

On each time step, surviving fish of each functional type and age-class are assumed to grow in length by an amount specified by equation (1). This results in an increase in weight

$$\Delta W = W_t - W_{t-5} = \alpha_1 L_t^{\alpha_2} - \alpha_1 L_{t-5}^{\alpha_2}$$

for each fish. This biomass must be acquired through predation. Thus it is assumed that, on each time step, an amount of biomass

$$\Sigma_i \frac{\Delta W}{C_{\text{assim}}}$$

is removed from the prey species in the model, where the summation index, i, runs over all fish and C_{assim} is the assimilation coefficient, or ratio of the increase in biomass of the consumers to the biomass removed from prey.

Each predator has its preferred prey. Both the small-fish functional type and the smaller size classes of the large-fish functional type prefer meso- and macro-invertebrates, while the larger size classes of the large piscivorous fish functional type prefer the smaller fish. If prey of the preferred type are available in sufficient

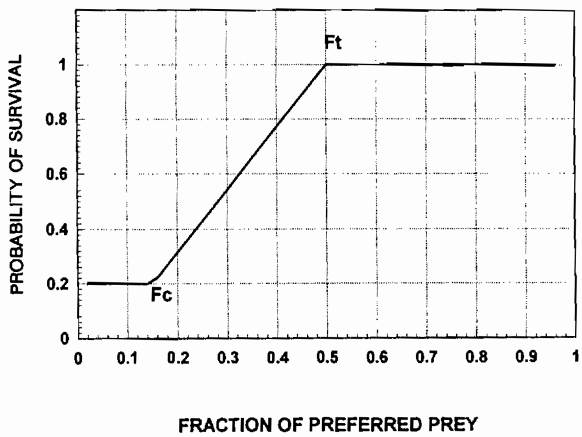

Figure 5. This figure shows the implementation of a density-dependent mortality effect on fishes of the two functional types. When the fraction of preferred prey types in the diet of the fish is above a certain level, there is no density-dependent mortality. When this fraction falls below the threshold level F_t in the figure, density-dependent survivorship during a particular time step starts to decline. If this fraction falls below a critical level, F_c, then survivorship is fixed at a minimum level.

quantity (high enough ratio of prey biomass to the biomass of all potential predators), then the biomass used for growth of the predator comes from those preferred prey. It is assumed here that if the preferred prey are not available in sufficient biomass, then some biomass comes from less desirable types of prey. The necessity of utilizing less desired prey is assumed to adversely affect survivorship. This relationship is depicted in Figure 5.

The interactions between the piscivorous-fish type and their small-fish type prey are modified in the marsh area. It is assumed that the marsh provides some protective cover for the smaller fish. Therefore, the piscivorous fish require a higher density of prey fish in the marsh than in the pond to achieve the same feeding rate.

3. Simulations

Simulations of the model were performed to examine the following general aspects of the behavior of the fish populations.

1. The dynamics of the fish population in the marsh portion of the spatial cell through a year as a function of the hydroperiod. Figure 6 shows six different water-depth scenarios through a single year, ranging from a scenario with a dry period of about five months (scenario a) to scenarios in which the spatial cell is flooded during the whole year (scenarios e and f). To eliminate any effect of initial conditions on the fish populations, the simulation was extended for 15 years, with the same seasonal pattern of water depth repeated each year in a given simulation.
2. The effect of droughts of various duration on the survival of fish in the marsh, and on their recovery after the water depths return to previous levels. Figure 7 shows two different patterns of drought imposed on an otherwise continuously flooded cell. The shorter drought period (thicker line) consisted of a small drydown in Year 7. The longer drought period (thinner line) consisted of a drought period lasting from Year 5 to Year 7, and large drydowns in the three succeeding years. Such prolonged droughts may be more common as a result of human modification of the system's hydrology.

Several results from the simulations were stored as output, including the following:

1. Total numbers of fish per square meter (summed over age-classes) for each functional group at monthly intervals (calculated separately for both the marsh and pond areas).
2. Total biomass of fish for each functional group in the whole 500 m × 500 m area on monthly intervals (calculated separately for both the marsh and pond areas).

4. Results

The model was used here to demonstrate qualitative modes of behavior that are important to understand and protect in conserving or restoring wetland ecosystems. An important property of many wetland ecosystems is the ability to produce high densities of fish over an appreciable portion of a year. Therefore, the response of the model to the different scenarios of water depth (or hydroperiods) shown in Figure 6, is especially important. Figure 8 shows the model predictions of densities (numbers per square meter, averaged over the entire 25-ha spatial cell) of the small type fish greater than 30 days of age throughout the year, for each of the scenarios, corresponding to hydroperiod scenarios a, b, c, d, e, and f of Figure 6. The population density for hydroperiods a and b reach a maximum of only slightly more than 1 fish/m^2 and slightly more than 2 fish/m^2, respectively. Apparently, a flooded period of only seven or eight months is not sufficient for large population growth. A strong periodicity is shown in the two

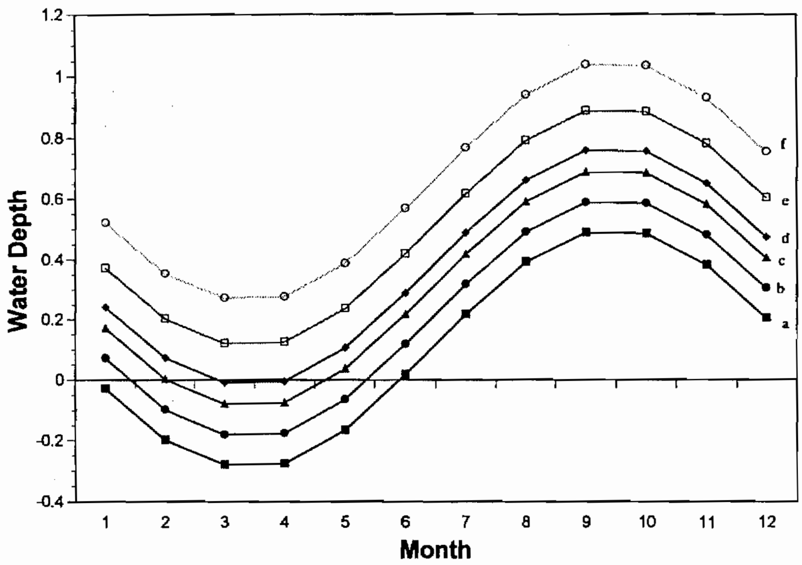

Figure 6. Six assumed intra-annual water depth scenarios for the spatial cell. Curves e and f represent cases in which the cell is flooded continuously, though at changing depths.

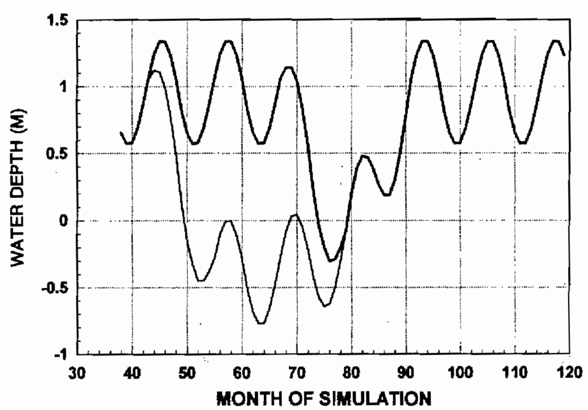

Figure 7. Water depth in cell for two assumed drought scenarios. The milder, one-year drought scenario is represented by the thicker line, and the more severe, three-year drought by the thin line.

intermediate scenarios, c and d, with maximum population densities toward the end of the flooded period of more than 10 fish/m^2. When the cell is flooded continuously, the populations of the small type fish fluctuate between about 13 and 20 fish/m^2. The reason for the seasonal changes in this case is that the lower trophic levels are undergoing seasonal variations.

Figure 9 shows the number densities of fish of the large functional-type, the piscivores, for the same scenarios. Their number densities are roughly three orders of magnitude smaller than those of the small functional-type (planktivorous) fish. However, the densities follow the same seasonal pattern of increase through the period of cell flooding. Note that under conditions of year-around flooding (scenarios e and f), the piscivores show a cyclic pattern. This is out of phase with the somewhat less accentuated cyclical pattern of the small fish type (Figure 8e, f). These coupled patterns appear to be predator-prey oscillations. A closer inspection of the age-class structure of the piscivores revealed higher reproduction following the peak in small fish densities, which led to a buildup of piscivore number density. Thus, the shift from situations with hydroperiods of less than a year (scenarios a through d) to situations with year-around flooding (scenarios e and f) not only resulted in a large increase in piscivore numbers in the marsh, but also a change of phase in the cyclic behavior of these numbers.

Additional simulations were performed in which large fish were removed from the simulations altogether to see whether that had a significant effect on the predicted population of small fish. There was little observable effect on the smaller fish densities in the marsh area. For the set of assumptions in this model, at least, piscivorous fish appear have no appreciable effect on smaller fish numbers, although yearly changes in numbers of small fish seem to be causing cycles in piscivore numbers in the year-around flooding conditions (scenarios e and f).

In the second simulation experiment, the spatial cell was subjected to a situation in which hydrology

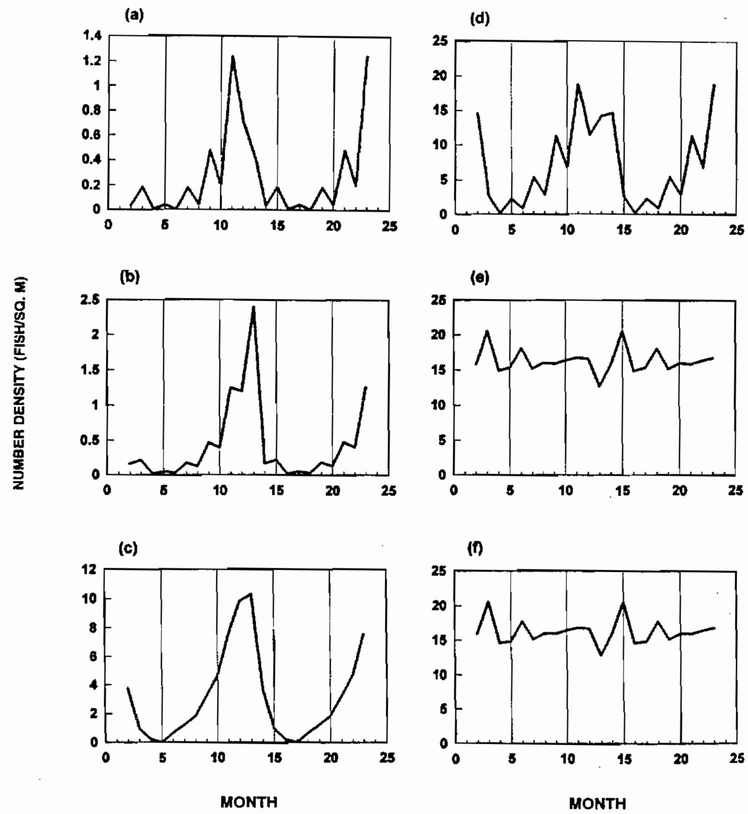

Figure 8. Densities (numbers/square meter) of the small functional type simulated through the year. For each of the six intra-annual hydrologic scenarios shown in Figure 6. The plots, (a), (b), (c), (d), (e), and (f) correspond to the small fish type densities for the similarly labelled curves in Figure 6.

changed from year to year. The purpose of this experiment was to determine the resilience of the small-fish population; that is, to determine how rapidly it could return to previous high levels following droughts of different levels of severity. Simulations over 15-year periods were performed under two different scenarios, shown in part in Figure 6. These scenarios are both sinusoidal within a year, but with a mean water level that changes. The thick curve represents a continuously flooded system that undergoes a four-month dry period in Year 7, while the thin curve represents a prolonged drought that starts in Year 5 and lasts into Year 7. There is a rapid reflooding and the seasonal cycle is back to the baseline pattern by the middle of Year 8.

In the drought experiment depicted in Figure 7, the population subjected to a three-year drought declines far below that subjected to only one year of drought, though it does not go to extinction. This is shown in Figure 10, where the natural log of the populations are plotted. The population subjected to a large drought is smaller than the other population by a factor of about 500 at Month 79. However, it recovers to within a factor of two or so within two months. After that, both populations recover to their baseline levels (for flooded conditions) within a year.

5. Discussion

The system studied here, that of fishes in a freshwater marsh that undergoes periodic flooding and drying, is conceptually simple. During periods of flooding, populations of small fishes invade the wetlands from ponds and other refuges and increase in size. The growth of the small fish type population continues until one of the following occurs: (1) resources in the flooded marsh become limiting, (2) populations of piscivorous fish (or other predators) increase and control the small fish, or (3) the next drydown of the marsh occurs. During drydowns, the fish retreat to ponds or other depressions.

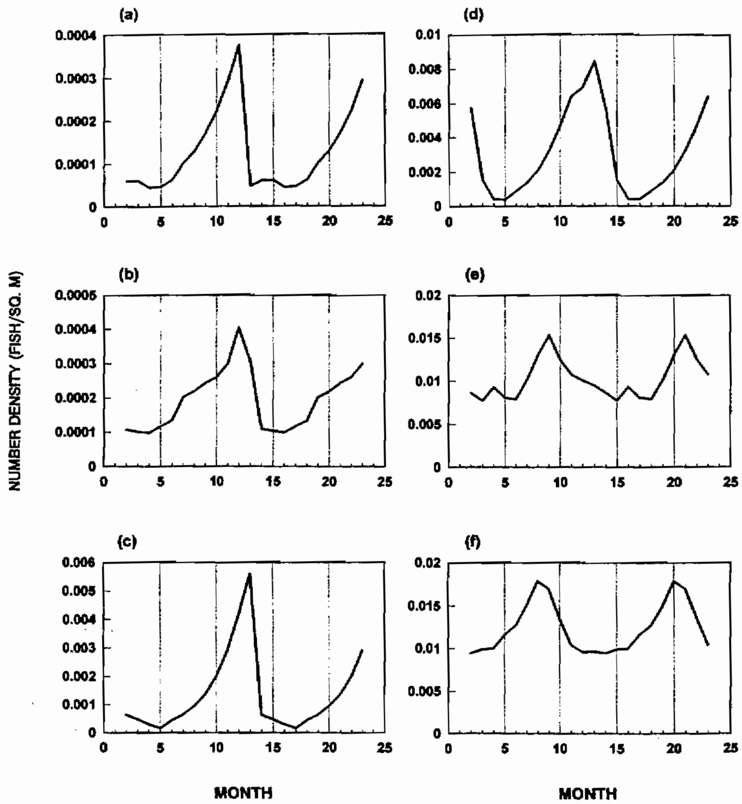

Figure 9. Densities (numbers/square meter) of the large, piscivorous functional type simulated through the year. For each of the six intra-annual hydrologic scenarios shown in Figure 6. The plots, (a), (b), (c), (d), (e), and (f) correspond to the large fish type densities for the similarly labelled curves in Figure 6.

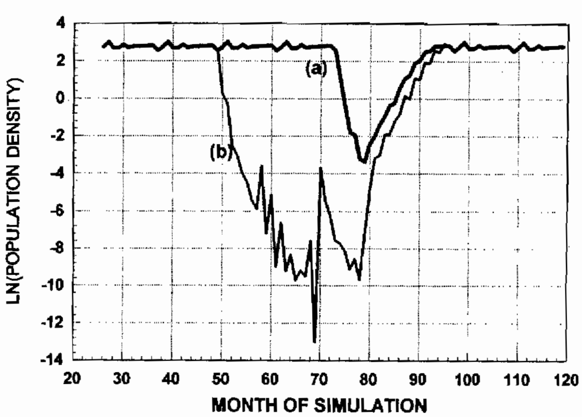

Figure 10. Natural logarithm of densities of small fish in marsh subjected to the drought scenarios shown in Figure 7: (a) a short, mild drought in Year 7 and a long drought extending over Years 5, 6, and 7.

While this hydrologically driven system is simple conceptually, many data needs became apparent when we modeled it quantitatively. A knowledge of the microtopography of the spatial cell is essential, because it determines the amount of refuge area that remains at decreasing water depths as the marsh dries. The fraction of fishes able to find refugia also had to be estimated. The life-history characteristics of the small fishes had to be known to predict the speed of recovery of the populations following reflooding. The resource base of the small fish had to be modeled (or else the effective carrying capacity estimated). Similar characteristics of the piscivorous fish, as well their ability to feed on smaller fishes in the complex marsh environment, had to be quantified.

Beyond these difficult assumptions that were incorporated into the model are aspects of the system that we did not even attempt to take into account. For example, it is possible that drydowns have broader effects than simply reducing the fish populations. The length and magnitude of a drydown may have an effect on lower trophic level productivity during the next period of flooding (Loftus & Eklund, 1994). We also simpified the system to small planktivorous and large piscivo-

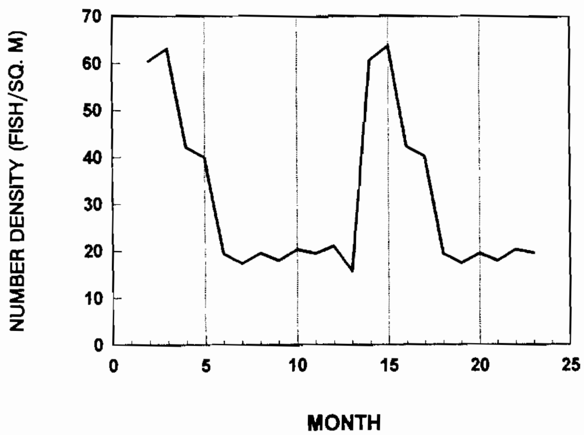

Figure 11. Density of small functional type fish in marsh through a year (corresponding to Figure 8a) when density is computed on the basis of fraction of area in the spatial cell flooded rather than the whole cell area. Note that the local fish number density in Month 3 is about 50 times higher than the density normalized on the size of the whole spatial cell.

rous fish interacting with a simple food base, ignoring other aspects of the food web.

Keeping in mind these serious caveats, we nonetheless believe that the model makes predictions that may be useful, particularly for roughly predicting the amount of biomass that may become available to higher trophic levels (in particular, to wading birds) during the marsh hydrologic cycle. For hydroperiods greater than about nine months, the populations of small fishes in the spatial cell built up to levels of 10 to 20 fish per square meter, or biomasses of close to a gram or so dry weight per square meter. These densities are measured on a whole-cell basis (25-ha in this model) and thus may be a serious underestimate of the local densities that actually become available to wading birds as water levels decline and the flooded area of the marsh shrinks. For example, Figure 11 recalculates the fish number density of Figure 8a, by normalizing it to the amount of area actually flooded. In this case, local densities as high as 6 small fish per square meter occurred, even though the density of fish on the whole-cell basis was less than two fish per cell. In the pond area, numbers of small fish up to several hundreds per square meter were predicted.

The model makes three further predictions that appear to us to be fairly robust in the model system. First, there appears to be a threshold of about nine or so months in the length of the hydroperiod. If the hydroperiod is less than this, the small fish population stays small, no more than a few fish per square meter. For longer hydroperiods, the fish population can reach levels of 10 to 20 fish per square meter by the end of the hydroperiod, roughly what the population would be under continuously flooding. The second prediction is that the large, piscivorous fish do not have a significant impact on small fish populations in the marsh, even though they do in the pond. The third prediction is that the repopulation of the marsh by small fishes following a drydown, even a prolonged drydown, occurs very rapidly, within a little less than a year (though this year could be a critical one for wading birds dependent on fish prey).

If the above predictions are, indeed, robust and general ones, then the prediction of the impact of fluctuating water levels on the numbers of small fishes, aggregated over species, in a marsh will be made much more simple. Intuitively, we cannot believe that the situation is so straightforward. Nevertheless, we believe the predictions are a useful starting point for more careful testing with models and for collection of field data.

The model described in this paper is intended to be general and not necessarily to apply in detail to a specific system. However, it is worthwhile to compare the results with available data where possible, to determine if the model at least approximates a real system. Data on the seasonal changes of fish number and biomass densities are available for some areas of Everglades National Park (Loftus & Eklund, 1994). Conveniently, these authors have divided the fishes they surveyed into the two types of large and small fishes that are used in the model.

Loftus & Eklund (1994) sampled fish populations in the Everglades over a period of several years, and found mean annual densities of the small-fish type to range from 15.5 to 17.1 fish/m^2 in the early part of the study and 30.2 to 34.5 in the later part of the study. This compares with values of about 5 to 15 small-type fish/m^2 in the model for the longer hydroperiod simulations. Loftus & Eklund (1994) estimated the mean annual density of large-type fishes at about 0.012 fish/m^2. The model densities ranged from about 0.005 to 0.013 for the longer hydroperiod simulations.

The empirical data of Loftus & Eklund (1994) showed strong seasonal oscillations, with the highest small-fish densities within a year approaching four or five times the lowest densities. This contrasts with the oscillations over a year in the model, where dry season densities dropped to a very small fraction of the peak densities. It may be that the model drydown periods were more severe, or at least more continuous, than those occurring in the Everglades areas sampled by Loftus & Eklund.

The model simulations are in general comparable with data from the field in the Everglades (Loftus & Eklund, 1994), even though the only part of the model that has been calibrated to data was that for the lower trophic levels. This indicates that the model is probably correctly transferring the energy into the two fish functional groups. Other aspects of model predictions, such as age-class distributions, cannot be tested at present because of lack of sufficient data.

The type of pulsed hydroperiod wetland simulated here is an important generic type that occurs in many places around the world, especially in the tropics and subtropics. The hydrologic pulsing is a key feature that can lead to the seasonal expansion and growth of prey populations and their subsequent concentration for higher trophic levels. Changes in the nature of the pulsing (timing, extent and duration of flooding) may affect this process of collection and concentration of biomass.

The results of this study have obvious implications for the conservation of species, such as wading birds and crocodilians, that depend on high concentrations of prey produced in pulsed hydroperiod wetlands. Humans are manipulating the water in many such systems, for urban and agricultural use as well as for flood control. A result of such manipulations is that hydroperiods will be changed. The effects of such changes can be devastating for wildlife and need to be understood better and predicted where possible. Modeling studies appear helpful in elucidating these effects.

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References

Browder, J. A., S. Black, P. Schroeder, M. Brown, M. Newman, D. Cottrell & P. Pope, 1981. Perspectives on the ecological causes and effects of the variable algal composition of southern Everglades periphyton. Report T-643, South Florida Research Center, Homestead, Florida, 110 pp.

Browder, J. A., D. Cottrell, M. Brown, M. Newman, R. Edwards, J. Yuska, M. Browder & J. Krakoski, 1982. Biomass and primary production of macrophytes in periphyton habitats of the southern Everglades. Report T-662, South Florida Research Center, Homestead, Florida, 49 pp.

Browder, J. A., P. J. Gleason & D. R. Swift, 1994. Periphyton in the Everglades: Spatial variation, environmental correlates and ecological implications. In: S. M. Davis & J. C. Ogden (eds), Everglades: The Ecosystem and Its Restoration, pp. 379–418. St. Lucie Press, Delray Beach, Florida.

Fennema, R. J., C. J. Neidrauer, R. A. Johnson, T. K. MacVicar & W. A. Perkins, 1994. A computer model to simulate natural Everglades hydrology. In: S. M. Davis & J. C. Ogden (eds), Everglades: The Ecosystem and Its Restoration, pp. 249–289. St. Lucie Press, Delray Beach, Florida.

Fleming, D. M., W. F. Wolff & D. L. DeAngelis, 1994. Importance of landscape heterogeneity to wood storks in Florida Everglades. Environmental Management 18: 743–757.

Hinrichson, D, 1995. Waterworld. The Amicus Journal 17: 23–27.

Loftus, W. F. & A. M. Eklund, 1994. Long-term dynamics of an Everglades small-fish assemblage. In: S. M. Davis & J. C. Ogden (eds), Everglades: The Ecosystem and Its Restoration, pp. 461–483. St. Lucie Press, Delray Beach, Florida.

Loftus, W. F., R. A. Johnson & G. Anderson, 1992. Ecological impacts of the reduction of groundwater levels in the rocklands'. In: J. A. Stafford & J. J. Simon (eds), Proceedings of the First International Conference on Groundwater Ecology, pp. 199–208. American Water Resources Association, Bethesda, Maryland.

Loftus, W. F. & J. A. Kushlan, 1987. Freshwater fishes of southern Florida. Bull. Fla. State Mus. Biol. Sci. 31: 147–344.

Ogden, J. C., 1994. A comparison of wading bird nesting colony dynamics (1931–1946 and 1974–1989) as an indication of ecosystem conditions in the southern Everglades. In: S. M. Davis & J. C. Ogden (eds), Everglades: The Ecosystem and Its Restoration, pp. 533–570. St. Lucie Press, Delray Beach, Florida.