FOOD WEB DYNAMICS IN A SEASONALLY VARYING WETLAND

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Abstract. A spatially explicit model is developed to simulate the small fish community and its underlying food web, in the freshwater marshes of the Everglades. The community is simplified to a few small fish species feeding on periphyton and invertebrates. Other compartments are detritus, crayfish, and a piscivorous fish species. This unit food web model is applied to each of the 10,000 spatial cells on a 100 x 100 pixel landscape. Seasonal variation in water level is assumed and rules are assigned for fish movement in response to rising and falling water levels, which can cause many spatial cells to alternate between flooded and dry conditions. It is shown that temporal variations of water level on a spatially heterogeneous landscape can maintain at least three competing fish species. In addition, these environmental factors can strongly affect the temporal variation of the food web caused by top-down control from the piscivorous fish.

1. **Introduction.** The huge flocks of wading birds in the Everglades are supported by a less conspicuous but nonetheless important food web, consisting principally of small fishes. They constitute an ecosystem component whose biomass is the major energy resource for higher trophic levels, especially wintering and breeding wading birds [5],[2]. The strongly seasonal rainfall pattern of this region creates a cycle of wet and dry seasons. Because of the flat landscape, relatively small differences in mean water level translate into major differences in the amount of wetted area and flooding duration, which affect the plant and animal communities. The wetland small-fish community is strongly influenced by seasonal hydrologic fluctuations [4],[6].

The Everglades ecosystem also poses important scientific questions. The coexistence of many fish species of similar small body size and resource use needs an explanation. Second, trophic chains will undergo regular dramatic changes in structure, as seasonal changes in water depth either limit or expedite the presence of larger food web components, such as planktivorous and piscivorous fish. If top-down effects (trophic cascades) are important in these trophic chains, dramatic changes may ensue as top trophic levels invade or leave parts of the hydroscape. How will this affect the seasonal dynamics of the food web?

Some earlier theory and modeling have already begun to address the first question. In an earlier paper it was assumed that the community of small fishes contained a spectrum of trade-offs in competitive ability and dispersal rates [3]. As vast areas of wetland are re-flooded each year, opportunistic fish species can disperse into and exploit those areas first, while other species appear better at dominating more permanently inundated areas of marsh. Species better at exploiting more stable areas should have higher reproductive and/or survival rates in long-hydroperiod areas, and they should be slower to disperse. As in some existing theories on "successional mosaics," according to our hypothesis, fish species populations move at different rates into newly opened (flooded) habitat, with the more competitive species moving more slowly than the more opportunistic ones. But this re-colonization process does not occur in randomly and asynchronously opened habitat patches, as in gap creation in forest systems, for example, but as large annual pulses during the seasonal flooding period. In addition, during the dry season, the recession of water forces all populations together into permanent or semi-permanent waterbodies. The gradual opening of new habitat by the rising water gives the more effectively dispersing fish species a temporary advantage, during which they can build in numbers before being subjected to competition by the other invaders. When the waters recede, the opportunistic fish are subjected again to heavy competition, but if they have built up high enough numbers, the species may persist. The capability of this mechanism for maintaining a number of competing fishes was demonstrated in [3].

Our goal here is to provide an extension of this earlier work on a competitive community to a minimal ecosystem model that should allow a large range of dynamics to be demonstrated under temporal and spatial variation. To do this we examine the dynamics of a small food web in which nutrients are recycled (primary producer, detritus, invertebrate detritivores, fish consumer of detritivores, nutrients) in a two-dimensional topography, for the case in which water levels rise and fall sinusoidally through the year. The fish are assumed to be migratory. A fraction of the fish is allowed to move up the gradient during rising water and down the gradient during falling water.

2. **Methods.** The model is spatially explicit on a 100 x 100 grid of square cells representing a segment of Everglades hydroscape, each cell assumed to be the size of a hectare. There are two basic parts to the model. The first is the structure of the food web and the equations describing fluxes between food web components. This set of equations is assumed to be the same for each of the 10,000 cells. The second part of the model is the set of rules for the movement of mobile species of the food web between the spatial cells.

2.1. **Differential equations of food web dynamics.** We first describe the food web. The basic food web structure of the model is shown in Figure 1. The fluxes between the food web components are described by a set of differential equations
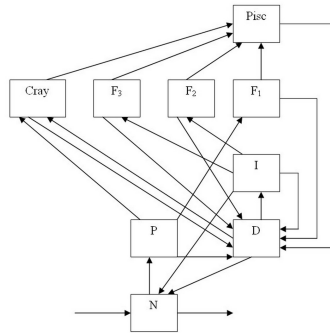
FIGURE 1. Schematic of the food web.

(See Table 1). Because this paper is meant as an overview of the model, which is still in development and testing, the equations are merely presented and model parameters are not discussed here. Variables and parameters are defined in Tables 2 and 3 respectively. All components are in nutrient units.

2.1.1. *Primary producers, $P(t)$*. This equation assumes an upper limit on periphyton growth rate, $Growth_{peri}$. It also assumes that there is an absolute upper limit on periphyton density, K_{peri}, which is simply a matter of space and light availability. It assumes a Monod function for nutrient limitation of periphyton growth. Finally, it assumes seasonality in periphyton growth and mortality.

2.1.2. *Detritus, $D(t)$*. This assumes an input from dying periphyton that is linearly related to periphyton density. It also assumes linear inputs from mortality of detritivores and three fish functional groups and crayfish. In addition, when there is consumption of fish on detritivores or fish on fish, then, because of incomplete digestion, there is some fractional input, $(1 - \eta)$, to detritus. There are nine terms here representing these inputs. Three terms are from the two fish species and crayfish that feed on detritivores, one from fish feeding on periphyton, one from crayfish feeding on periphyton, and four from piscivorous fish feeding on the three fish species and crayfish. The final three terms represent, respectively, the decomposition of detritus, releasing nutrients, and the feeding of detritivores and crayfish on the detritus. The consumption by detritivores is assumed to be donor-dependent on the amount of detritus.

2.1.3. *Invertebrate detritivores, $I(t)$*. There is a donor-dependent input from detritus and a loss due to mortality. There are two losses to consumption, from each of the two invertebrate consumer fish species.

2.1.4. *Fish feeders on periphyton, $F_1(t)$*. These fish are exclusively herbivores.

2.1.5. *Fish feeders on invertebrates, $F_2(t)$ and $F_3(t)$*. These fish are competing for the detritivore prey.

2.1.6. *Crayfish, $Cray(t)$*. These feed on detritus and periphyton.

2.1.7. *Piscivorous fish, $Pisc(t)$*. These feed on all other fish species, and on crayfish.

2.1.8. *Nutrients.* There is an external input, $Input_n$, to the nutrient compartment, which is due to the input of new water from upstream. There is also internal recycling of nutrients from decomposing detritus. There is uptake by periphyton and loss due to washout by water exiting the local system. Nutrients are assumed to be conserved in the model.

<div align="center">Table 1. Equations of the model.</div>

Primary producer $P(t)$ (periphyton), (in nutrient units):

$$\frac{dP(t)}{dt} = Growth_{peri} * Seasonal_1(t)\left(1 - \frac{P(t)}{K_{peri}}\right)\frac{P(t)N(t)}{k_{nutr}+N(t)}$$
$$-m_{peri} * Seasonal_1(t)P(t)$$
$$-Cons_{peri-by-invert}Seasonal_1(t) * P(t)\left(\frac{P(t)I(t)}{b_{invert}+P(t)}\right)$$
$$-Cons_{peri-by-fish1}Seasonal_1\left(\frac{P(t)F_1(t)}{b_{fish}+P(t)}\right)$$

Detritus $D(t)$, (in nutrient units):

$$\frac{dD}{dt} = m_{peri}Seasonal_3(t)P(t) + m_{inverti}Seasonal_3(t)I(t)$$
$$+m_{fish1}Seasonal_1(t)F_1(t) + m_{fish2}Seasonal_1(t)F_2(t)$$
$$+m_{fish3}Seasonal_1(t)F_3(t) + m_{cray}Seasonal_1(t)Cray(t)$$
$$+m_{pisc}Seasonal_1(t)Pisc(t)$$
$$+(1-\eta_{invert})\ Seasonal_3(t)P(t)\left(\frac{Cons_{peri-by-invert}I(t)}{b_{invert}+P(t)}\right)$$
$$+(1-\eta_{fish})\ Seasonal_1(t)P(t)\left(\frac{Cons_{peri-by-fish1}F_1(t)}{b_{fish}+P(t)}\right)$$
$$+(1-\eta_{fish})\ Seasonal_1(t)I(t)\left(\frac{Cons_{invert-by-fish2}F_2(t)}{b_{fish}+I(t)}\right)$$
$$+(1-\eta_{fish})\ Seasonal_1(t)I(t)\left(\frac{Cons_{invert-by-fish3}F_3(t)}{b_{fish}+I(t)}\right)$$
$$+(1-\eta_{fish})\ Seasonal_1(t)I(t)\left(\frac{Cons_{peri-by-cray}Cray(t)}{b_{crayt}+I(t)}\right)$$
$$+(1-\eta_{fish})\ Seasonal_1(t)F_1(t)\left(\frac{Cons_{fish1-by-pisc}Pisc(t)}{b_{fish}+F_1(t)}\right)$$
$$+(1-\eta_{fish})\ Seasonal_1(t)F_2(t)\left(\frac{Cons_{fish2-by-pisc}Pisc(t)}{b_{fish}+F_2(t)}\right)$$
$$+(1-\eta_{fish})\ Seasonal_1(t)F_3(t)\left(\frac{Cons_{fish3-by-pisc}Pisc(t)}{b_{fish}+F_3(t)}\right)$$
$$+(1-\eta_{fish})\ Seasonal_1(t)Cray(t)\left(\frac{Cons_{cray-by-pisc}Pisc(t)}{b_{fish}+Pisc(t)}\right)$$
$$-Seasonal_1(t)D(t)\frac{Cons_{det\,ritus\_by\_inverts}(I(t)}{b_{invert}+D(t)}$$
$$-Seasonal_1(t)D(t)\frac{Cons_{det\,ritus\_by\_crayfish}Cray(t)}{b_{cray}+D(t)} - decomp_{det\,ritus}D(t)$$

Invertebrate detritivores, $I(t)$, (in nutrient units):

$$\frac{dI(t)}{dt} = Cons_{det\,ritus-bv-inverts}Seasonal_1(t)D(t)$$
$$- m_{invert}\ Seasonal_3(t)D(t)$$
$$+\eta_{invert}\ Cons_{peri-by-inverts}Seasonal_3(t)\ P(t)$$
$$-Seasonal_1(t)I(t)\left(\frac{Cons_{invert-by-fish2}F_2(t)}{b_{fish}+I(t)}\right)$$
$$-Seasonal_1(t)I(t)\left(\frac{Cons_{invert-by-fish3}F_3(t)}{b_{fish}+I(t)}\right)$$
$$-Seasonal_3(t)\ Excrete_{invert}(t)\ I(t)$$

Fish feeders on periphyton, $F1(t)$, (in nutrient units):

$$\frac{dF_1}{dt} = \eta_{fish} \; Seasonal_1(t)P(t) \left(\frac{Cons_{peri-by-fish1}F_1(t)}{b_{fish}+P(t)} \right)$$
$$- m_{fish1} \; Seasonal_1(t) \; F_1(t)$$
$$- Seasonal_1(t)F_1(t) \left(\frac{Cons_{fish1-by-pisc}Pisc(t)}{b_{fish}+F_1(t)} \right)$$

Fish feeders on invertebrates, $F2(t)$ and $F3(t)$ (in nutrient units):

$$\frac{dF_2}{dt} = \eta_{fish} \; Seasonal_1(t) \; I(t) \left(\frac{Cons_{invert-by-fish2}F_2(t)}{b_{fish2}+F_2(t)} \right)$$
$$- m_{fish2} \; Seasonal_1(t)F_2(t)$$
$$- Seasonal_1(t) \; F_2(t) \left(\frac{Cons_{fish2-by-pisc}Pisc(t)}{b_{fishp}+F_2(t)} \right)$$
$$\frac{dF_3}{dt} = \eta_{fish} \; Seasonal_1(t) \; I(t) \left(\frac{Cons_{invert-by-fish3}F_3(t)}{b_{fish3}+I(t)} \right)$$
$$- m_{fish3} \; Seasonal_1(t)F_3(t)$$
$$- Seasonal_1(t) \; F_3(t) \left(\frac{Cons_{fish3-by-pisc}Pisc(t)}{b_{fishp}+F_3(t)} \right)$$

Crayfish, $Cray(t)$ (in nutrient units):

$$\frac{dCray(t)}{dt} = \eta_{fish} \; Seasonal_1(t) \; D(t) \left(\frac{Cons_{detritus-by-cray}Cray(t)}{b_{fish}+D(t)} \right)$$
$$- m_{cray} \; Seasonal_1(t) \; Cray(t)$$
$$- Seasonal_1(t) \; Cray(t) \left(\frac{Cons_{cray-by-pisc}Pisc(t)}{b_{fish}+Cray(t)} \right)$$

Piscivorous fish $Pisc(t)$, (in nutrient units):

$$\frac{dPisc(t)}{dt} = -m_{fish3} \; Seasonal_1(t) \; F_3(t)$$
$$+\eta_{fish}Seasonal_1(t) \; F_1(t) \left(\frac{Cons_{fish1-by-pisc}Pisc(t)}{b_{fishp}+F_1(t)} \right)$$
$$+\eta_{fish}Seasonal_1(t) \; F_2(t) \left(\frac{Cons_{fish2-by-pisc}Pisc(t)}{b_{fishp}+F_2(t)} \right)$$
$$+\eta_{fish}Seasonal_1(t) \; F_3(t) \left(\frac{Cons_{fish3-by-pisc}Pisc(t)}{b_{fishp}+F_3(t)} \right)$$
$$+\eta_{fish}Seasonal_1(t) \; Cray(t) \left(\frac{Cons_{cray-by-pisc}Pisc(t)}{b_{fishp}+Cray(t)} \right)$$

Nutrients:

$$\frac{dN(t)}{dt} = Input_n + decomp_{detritus} \; Seasonal_3(t) \; D(t)$$
$$- Growth_{peri} \; Seasonal_1(t) \; (1 - \frac{P(t)}{K}) \left(\frac{P(t)N(t)}{k_1+N(t)} \right) - Loss_N N(t)$$

Table 2. Variables of the model.

Variable	Units	Definition
P	g nutrient m^{-2}	Periphyton
D	g nutrient m^{-2}	Detritus
I	g nutrient m^{-2}	Invertebrate detritivores
F_i (i = 1,3)	g nutrient m^{-2}	Small fish species populations
$Cray$	g nutrient m^{-2}	Crayfish
$Pisc$	g nutrient m^{-2}	Piscivorous fish
N	g nutrient m^{-2}	Nutrients

Table 3. Parameters of the model.

Parameter	Units	Definition
$Growth_{peri}$	g g^{-1} day^{-1}	Maximum periphyton growth
m_{peri}	day^{-1}	Mortality rate coefficient
m_{invert}	day^{-1}	”
m_{fish1}	day^{-1}	”
m_{fish2}	day^{-1}	”
m_{fish3}	day^{-1}	”
m_{pisc}	day^{-1}	”
m_{cray}	day^{-1}	”
k_{nutr}	g m^{-2}	Half-saturation of nutrient uptake
K_{peri}	g m^{-2}	Carrying capacity of periphyton
b_{fish}	g m^{-2}	Population regulation coeff., fish
b_{invert}	g m^{-2}	Population regulation coeff., inverts
$Cons_{peri-by-invert}$	g g^{-1} day^{-1}	Consumption rate coefficient
$Cons_{peri-by-fish1}$	g g^{-1} day^{-1}	”
$Cons_{invert-by-fish2}$	g g^{-1} day^{-1}	”
$Cons_{invert-by-fish3}$	g g^{-1} day^{-1}	”
$Cons_{fish1-by-pisc}$	g g^{-1} day^{-1}	”
$Cons_{fish2-by-pisc}$	g g^{-1} day^{-1}	”
$Cons_{fish3-by-pisc}$	g g^{-1} day^{-1}	”
$Cons_{cray-by-pisc}$	g g^{-1} day^{-1}	”
η_{invert}		Assimilation coefficient
η_{fish}		”
$decomp_{detritus}$	day^{-1}	Decomposition rate
$Input_n$	g day^{-1}	External nutrient input
$Loss_n$	day^{-1}	Loss rate of nutrient from system

2.2. Seasonality. Here the factors $Seasonal_i(t)$ simply mean that these rates are adjusted according to whether the cell is flooded or not. This representation of seasonality can be elaborated to whatever degree of detail is required, but at present are simply binary.

2.3. Movement of organisms. There are three sources of movement: (1) diffusion, (2) movement out of cells that are drying, and (3) movement into cells that are becoming flooded.

2.3.1. *Non-fish organisms.* It is important that all organisms be able to start to generate populations when a cell is reflooded. This would be impossible to do if there were absolutely no biomass in the cell to start. This difficulty is handled in two ways. One is for cells to have some residue of a population remaining even when they are dry. This is the case for periphyton in the model. We assume that when a cell dries, initially 5% of the remaining periphyton is still alive (in small ponds, etc.), though that amount continues to decline through mortality. Thus, when the cell refloods, periphyton biomass is able to grow rapidly.

Invertebrate detritivores are assumed able to move into a newly flooded cell from surrounding cells. At the moment, a total of 10% of the detritivore biomass from prior flooded cells are able to move into the newly flooded cell. This is probably too high, but it is certainly necessary to have either some immigration or for a residue

population to remain; otherwise, detritivores would not recover fast enough in a newly flooded cell.

Similarly, when a cell is drying, some fraction of the detritivores is assumed able to migrate to cells that are still wet. At the moment this is set to zero in the absence of information.

2.3.2. *Fish.* Diffusion: It is assumed that there is some daily diffusion between cells of all fish species. It is assumed at present that all fish have a fractional transfer rate between cells each day, of 0.05 of the population of a cell. The smaller fishes can move into any cell that is greater than 4 cm in depth, while the larger, piscivorous fish can transfer only when the depth of water in the recipient cell is greater than 6 cm.

Cell drying: When a cell effectively dries (falls below 4 cm in depth for smaller fish and 6 cm in depth for piscivorous fish) it is assumed that 40% of the fish move out of that cell and move to the adjacent cell that has the deepest water. This is the same for the fish that feed on detritivores and the piscivorous fish. The fish that remain stranded in a cell die and become detritus.

Cell reflooding: When a cell refloods, smaller fish can move in from an adjacent cell when the depth of that cell reaches 4 cm. At present, a total of 20% of the total fish from each of the surrounding already flooded cells is able to move to the newly flooded cell. Piscivorous fish are assumed able to move to a reflooded cell only after it has reached 6 cm, and only 20% of the fish from a given adjacent already flooded cells move to the reflooded cell.

This model is very simple at present, but it is necessary to keep things simple at first, as it is necessary to make sure that the model is working correctly on the landscape, which is easier when the model is simple. We want to eventually get this model to be a fairly good approximation of what we think the biomass-nutrient dynamics of the marsh system are like.

2.4. **Results.** Two preliminary studies have been done with the model. The objective of the first was specifically aimed at a test of competition dynamics of the small fish species and the second was an examination of trophic dynamics.

The first of these studies was done using the model shown in Figure 1, but simplified by omission of the crayfish and piscivores, using a simple landscape like the one in Figure 2. The water level was allowed to vary sinusoidally through the year, so that the amount of landscape flooded varied substantially through a year. As a result, the components of the food web varied both temporally and spatially. Figure 3 shows the variation in periphyton, detritus, detritivores, and fish, averaged over the whole landscape, over a year.

Figure 4 shows one-dimensional projections of the densities of three different fish species along an elevation gradient similar to that in Figure 2 with the elevation increasing towards the left. At the extreme right-hand side the land is permanently flooded, whereas at the left extreme it is flooded only briefly. The 12 plots show the density profiles of the three competing fish species at monthly intervals. In the top left plot, water level has just passed its maximum and is starting to decline. The three species differ in their competitive and dispersal abilities. Note that one species disperses very little, but maintains high density in the areas that are continuously or almost continuously flooded. The best disperser, and poorest competitor, almost disappears when the water level contracts during the dry season, but is able to
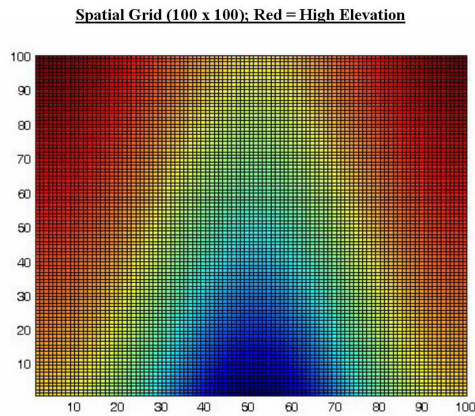
FIGURE 2. Example of a simple landscape used for study of model. Here the lowest elevation is 0 meters and the highest is 0.8 meters.
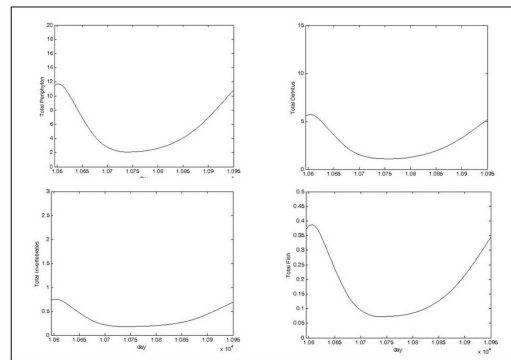

FIGURE 3. Results of Simulation 1 of food web, showing periphtyon, detritus, invertebrates, and total over three small fish species, each averaged over the whole hydroscape. Period of simulation is one year.

rapidly disperse when flooding recurs and builds up a large population by feeding on resources that it can monopolize. The intermediate species finds a niche in between these two. This shows the capability of at least three species utilizing the same resource to coexist.

DeAngelis et al.[3] did not consider a whole food web, and food web structure constitutes another basic aspect of ecological theory. One of the key elements of food web theory is the possible occurrence of top-down effects, or trophic cascades. A basic question in a strongly varying system, then, is how does this "top-down effect" manifest itself in a system in which the top consumer may be periodically affected, even temporarily removed, by changes in the abiotic factor of water depth? Some simple insights on how aquatic trophic cascades are affected by seasonal water level variations along an elevation gradient may be seen by replacing the gradual gradient by two elevation levels. The lower elevation is continually flooded such that three trophic levels can always co-occur: primary producers, an herbivorous fish,
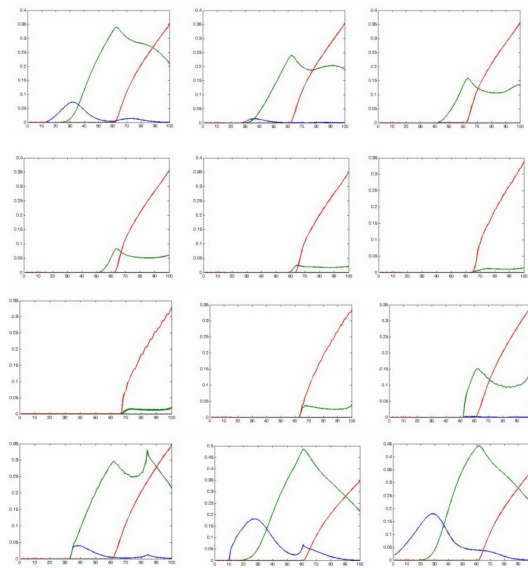
FIGURE 4. First panel shows highly flooded conditions, followed by panels showing gradual drying and then reflooding. Species 1 (blue) = poor competitor, good disperser, Species 2 (red) = good competitor, poor disperser, Species 3 (green) = intermediate.

and a piscivorous fish population. The higher elevation is always flooded such that the two lower trophic levels are always present, but the larger piscivorous fish may only be present during part of the year, when the water level is high enough to allow them to invade. This situation was studied by simplifying our model (Figure 1) to exclude the invertebrate and contain only the chain of periphyton, a fish that grazes periphyton, and the piscivorous fish. The nutrient concentration was assumed fixed.

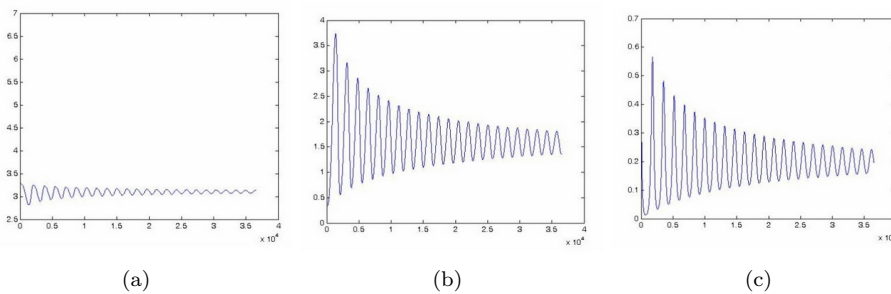(a)   (b)   (c)

Figure 5. Simulation of (a) periphyton, (b) herbivorous fish, and
(c) piscivorous fish, in a simple three-level chain along an elevation
gradient with two levels. It is assumed that the water depth at the
higher elevation is too shallow for invasion of the piscivore. The
two dimensional chain in the high elevation zone (not shown) is
completely stable, while the three dimensional chain in the low
elevation zone (shown) has a stable focus (which can be demonstrated
by carrying the simulation further in time). Period of simulation
is ten years

(d)   (e)   (f)
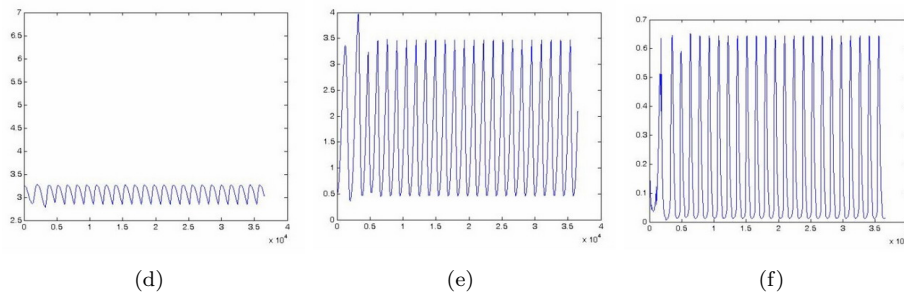
Figure 6. Simulation of (a) periphyton, (b) herbivorous fish, and
(c) piscivorous fish, in a simple three-level chain along an elevation
gradient with two levels. It is assumed that the water depth at the
higher elevation is high enough for part of the year for the piscivore
to invade. The trophic chains in both zones are unstable. The three
trophic levels of the chain in the low elevation zone are shown.
Period of simulation is ten years.

This simplified situation is complex enough to allow a variety of dynamics to occur. However, here we present only one of many varied outputs. The parameters were first fixed such that, if the piscivorous fish were not allowed to move into the shallower zone, the dynamics in both the shallow (periphyton-fish) and deep (periphyton-fish-piscivore) zones were relatively stable (as can be shown by carrying the simulations further in time than shown in Figure 5). When a sizeable fraction of the piscivorous fish was allowed to move into the shallow zone part of the year, however, the whole system underwent drastic limit cycle oscillations (Figure 6).

2.5. **Discussion.** The present model simulations extend earlier work to a more realistic model. In [3] a simpler variation on this model allowed five species to coexist along an elevational gradient with seasonally varying water depth. It was hypothesized that maintenance of a diverse wetland fish community could be related to current ecological theory on non-equilibrium communities. Environmental fluctuations are often proposed as means for maintaining richness in a dynamic community by preventing competitively dominant species from eliminating others. Chesson [1] reviewed the mathematical models incorporating hypothesis for how environmental fluctuations could promote diversity in non-equilibrium communities, noting that the fluctuations effectively provide distinct niches for the competing species. These circumstances may occur when the competing species have tradeoffs in key

physiological and/or behavioral traits that allow the relative advantages to alternate among species in a fluctuating environment. An example of such trade-offs is that between early invading opportunist plant species in randomly occurring forest canopy gaps, which are later out-competed by species that are slower to invade, but more shade tolerant.

Our conceptual model for the southern Florida wetland fish community contains the primary elements of resource fluctuations and spatial dispersal, found in many non-equilibrium hypotheses of biodiversity. Fish species populations move at different rates into newly opened (flooded) habitat, with the more competitive species moving more slowly than the more opportunistic ones. But this re-colonization process does not occur in randomly and asynchronously opened habitat patches, as, for example, in gap creation in forest systems, but as large annual pulses during the seasonal flooding period. In addition, during the dry season, the recession of water forces all populations together into permanent or semi-permanent waterbodies.

The initial study of a simplified food chain indicates the potential complexity resulting from including spatial heterogeneity and seasonal water level fluctuations. As noted, one of our objectives is to address the question of how the "top-down effect" manifests itself in a system in which the top consumer can only periodically invade parts of the space. Here, one possible dynamic effect is observed, that the periodic invasion of the higher elevation area triggers severe limit cycles in a system that is more stable (at most has only smaller cycles) without the movement of piscivores. This and other results will be examined in more detail in later work.

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