Ecological Applications, 12(6), 2002, pp. 1740–1754

ASSESSING CUMULATIVE IMPACTS OF LEVEES AND DAMS ON FLOODPLAIN PONDS: A NEUTRAL-TERRAIN MODEL APPROACH

SARAH E. GERGEL[1]

Zoology Department/Center for Limnology, University of Wisconsin, Madison, Wisconsin 53706 USA

Abstract. Nearly all large rivers and their floodplains in the Northern Hemisphere are subject to multiple disturbances such as levees, impoundments, channelization, dams, and changes in land use. Isolating the relative impact of different disturbances is difficult when the combined effects are nonadditive. I developed a ''neutral-terrain model'' to examine the cumulative impacts of levees and dams on the hydroperiod of ponds and wetlands that form throughout floodplains after flood events. Using simulated floods of different magnitude, I address two major questions: (1) What is the relative influence of levees vs. dams on the duration and abundance of temporary ponds and wetlands? (2) Are the cumulative effects of levees and dams additive, synergistic, or antagonistic? Levees decreased the area occupied by temporary ponds (as compared to the natural scenario), until the levee was breached by large-magnitude events. When the levee was breached, no differences were found between the natural- and levee-floodplain scenarios. A simulated upstream dam decreased, increased, or had no effect on the area occupied by temporary ponds, depending on flood magnitude. Synergistic interactions between levees and dams were apparent for larger floods, where the reduction in flood stage caused by an upstream dam prevented levee breaching. Lastly, I introduce a qualitative framework for understanding the impacts of levees and dams on the duration of floodplain ponds. I also discuss the applications of this new three-dimensional simulation modeling technique, neutral-terrain modeling, as a tool for addressing spatial aspects of watershed and floodplain questions.

Key words: dams; flood magnitude; floodplain; levees; neutral-terrain model; temporary pond; wetlands; Wisconsin River.

INTRODUCTION

The ecological impacts of single disturbances and stresses have long been of interest to ecologists. However, less attention has been paid to the effects of multiple disturbances (Bedford and Preston 1988, Paine et al. 1998, Breitburg et al. 1999) although many ecosystems and organisms are impacted by multiple disturbances and stressors (Schindler at al. 1996, Yan et al. 1996, Paine et al. 1998). In addition, because anthropogenic disruptions of ecosystems are pervasive and generally increasing in frequency and magnitude (Holling and Sanderson 1996, Vitousek et al. 1997), multiple perturbations to ecosystems will likely become more common (Paine et al. 1998). Isolating the relative impact of different types of concurrent disturbances is difficult. Furthermore, predicting the effects of several disturbances is especially challenging when the combined effects are interactive or nonadditive. Nonadditive effects of disturbances can be synergistic (have an impact greater than the summed individual disturbance effects) or antagonistic (produce less disruption than the summed individual disturbance effects).

Large rivers and their floodplains are often subject to multiple disturbances. In the northern hemisphere, nearly all major rivers have been altered by levees, impoundments, channelization, dams, and/or upland changes in land use (Potter 1991, Dynesius and Nilsson 1994, Power et al. 1995, Nilsson et al. 1997, Vitousek et al. 1997, Fitzpatrick et al. 1999). In the U.S., 98% of rivers are regulated (Vitousek et al. 1997), and 60% of the world's stream flow was expected to be regulated by the year 2000 (Petts 1989). There are ~17 000 km of levees in the upper Mississippi River basin (Tobin 1995) and an estimated 40 000 km of levees, floodwalls, embankments, and dikes in the USA (Johnston Associates 1989). By reducing peak flows, dams can reduce the frequency and amount of overbank flooding. Dams also interrupt downstream sediment transport and upstream fish migration (Sparks 1995). Levees prevent the lateral flow of sediment, nutrients, and organisms between rivers and their floodplains and can also increase flood heights (i.e., stage) for a given discharge (Sparks 1995). Levees and dams are ubiquitous and cooccur in many regions (e.g., the Upper Mississippi, USA; the Yellow River, China).

Here, I examine the cumulative impacts of levees and dams on temporary ponds and wetlands that form throughout floodplains after flood events. Floodplain ponds and wetlands are important habitat for many taxa. The range in duration of these habitats, from high-

Manuscript received 30 October 2000; revised 28 September 2001; accepted 11 March 2002.

[1] Present address: National Center for Ecological Analysis and Synthesis, 735 State St., Suite 300, Santa Barbara, California 93101 USA.

ly ephemeral to permanent, influences the abundance and distribution of organisms, as well as the ecosystem functions occurring in ponds and wetlands that are of value to society. Because dams and levees alter many aspects of the flood regime along river margins, they likely impact the availability and hydroperiod of wetland habitats. Furthermore, hydroperiod is a frequently used integrator of wetland function and hydrology (Brinson 1993, Mitsch and Gosselink 1993). Thus, changes in hydroperiod can provide a useful and direct measure of the impacts of levees and dams on these habitats.

Temporary ponds and wetlands are used by a wide variety of species from waterfowl, fish, frogs, salamanders, and a wide range of aquatic invertebrates (Dodd 1992, Werner and McPeek 1994, Murkin et al. 1997). Furthermore, the gradient in hydroperiod across a landscape (from permanent to temporary ponds) may be important to promoting the regional diversity of aquatic organisms. Aquatic invertebrates, plants, and amphibians segregate along a hydroperiod gradient (Schneider and Frost 1996, Corti et al. 1997, Skelly et al. 1999, Casanova and Brock 2000). Furthermore, in aquatic habitats from many regions (e.g., subalpine wetlands, upper Atlantic Coastal Plain, South Carolina, Mississippi River floodplain, lower Michigan) there is an important, covarying gradient of pond duration and predation risk in aquatic habitats (Schneider and Frost 1996, Wellborn et al. 1996, Corti et al. 1997, Leeper and Taylor 1998, Snodgrass et al. 1999, Wissinger et al. 1999), as many taxa appear to rely on short hydroperiod wetlands to escape predation from dragonfly larvae, fish, bullfrogs, and salamanders abundant in more permanent habitats. Wetland conservation plans should emphasize conservation of the entire hydroperiod gradient (Murkin et al. 1997, Williams 1997, Snodgrass et al. 2000*b*).

Hydroperiod also influences ecosystem processes in by ponds and wetlands that are valuable to society, such as flood control. Simulations by Potter (1994) found that quick-draining wetlands did not attenuate overbank flooding. These wetlands behaved similarly to flashy, urban sewer systems, promoting quick runoff and therefore not increasing the storage time of floodwaters on the floodplain. Permanent, slow-draining wetlands were not very useful for flood control, as they were likely to be at least partially full at the time of a flood, and thus unable to store more water. Potter (1994) concluded that wetlands of intermediate duration were most valuable for flood control, as they drained quickly enough to likely be empty before the next flood, but slow enough to attenuate runoff. Lastly, the duration of wetlands can also influence elemental cycling (e.g., mercury; Snodgrass et al. 2000*a*) and the abundance of pests and disease vectors (e.g., mosquitoes).

Dams and levees may modify the duration of floodplain ponds along large rivers. The water budgets of aquatic floodplain habitats are controlled by groundwater, precipitation, evapotranspiration, and overbank flooding. Dams and levees can alter the amount, extent, and timing of overbank flooding. Through a decrease in peak flows, dams can reduce the frequency of overbank inundation and decrease the area inundated during a flood. Levees also influence the spatial variability of floods by reducing the extent of the landscape inundated. Generalizations regarding the relative and cumulative impacts of levees and dams on the hydroperiod gradient throughout a floodplain remain largely unexplored.

Here, I develop a model of the effects of a flood-control levee and an upstream dam on the duration and relative abundance of ponds throughout simulated floodplain landscapes. Using simulated flood events, I address two major questions: (1) What is the relative influence of levees vs. dams on the duration and abundance of temporary ponds and wetlands? (2) Are the cumulative effects of levees and dams additive, synergistic, or antagonistic? A primary goal is to create a general framework for understanding the impacts of levees and dams on floodplain systems. A secondary goal is to introduce a new three-dimensional simulation-modeling technique, ''neutral-terrain modeling,'' as a tool for addressing spatial, watershed, and floodplain-level questions. This neutral modeling approach is necessary for the manipulation and replication of landscape scenarios, and the three-dimensional terrain model approach is necessary for addressing the spatial dynamics of flooding.

Methods

I developed a neutral-terrain model to determine the independent and cumulative impacts of dams and levees on the number of and area occupied by floodplain ponds of different duration after floods. Neutral landscape models are a well-developed tool of landscape ecology for exploring the theory behind land-use change, the movement of terrestrial species, and the spread of disturbance (Gardner et al. 1987, With and King 1997). Represented by a gridded map of cells (or pixels), a neutral landscape model can be likened to a statistical distribution (e.g., a *t* distribution or a chi-square distribution) used for data comparison. In the case of neutral-landscape models, the distribution is spatial: clumped, fragmented, random, etc. This spatial structure can be manipulated and replicated to approximate a range of values for simple measures of landscape structure such as the amount or arrangement of cover types. Here I create a new type of neutral landscape model, a neutral-terrain model, to mimic the terrain of a floodplain landscape typical of the upper Midwest. This neutral-terrain model incorporates three-dimensional information regarding topography to the original two-dimensional design of neutral landscape models. This neutral-terrain modeling approach is necessary for the manipulation and replication of land-

FIG. 1. The state of Wisconsin showing the Wisconsin River watershed. The calibration landscapes were obtained from the circled area.

scape scenarios. Furthermore, this type of terrain model realistically represents the fractal size distribution of floodplain ponds.

The model is parameterized from a reach of the Wisconsin River (Fig. 1) in the upper Midwest, USA. This area is representative of areas throughout the upper Midwest that have been impacted by dams and levees. Levees and dams have been in place in this area for nearly a century (Gergel et al. 2002). Several dam-removal projects are underway throughout the state of Wisconsin, and levee removal is being debated for this reach of the Wisconsin River. The topographic relief of the floodplain along this study reach is used to parameterize replicated, simulated floodplains. Different magnitude floods are simulated on these landscapes to predict the duration of resulting ponds and wetlands. I explore the effects of altered flood regimes for four scenarios: (1) natural, free-flowing conditions, (2) an upstream dam, (3) a levee, and (4) both a dam and a levee. This model is not designed to predict precisely the duration of any particular pond. Rather, this model is a heuristic tool for exploring spatial aspects of the hydroperiod gradient across a floodplain, in a manner not possible without a simulation model.

Floodplain terrain

Floodplain terrain was simulated using areas of the Wisconsin River as a frame of reference (Fig. 1). Geographic Information System (GIS) data from two 1500 $\times$ 1500 m areas of the Wisconsin River floodplain were used as ''calibration landscapes'' to bracket a range of values describing floodplain topography (Fig. 2). These two areas are relatively unimpacted by features such as roads, agriculture and artificial drainage canals that could alter the natural topographic relief. I determined three general features of these two calibration landscapes: (1) the proportion of the landscape occupied by different elevation classes, (2) the proportion of the landscape occupied by permanent standing water, and (3) the spatial autocorrelation (or clumpiness) of the topography. The mean values of these features were used to create the replicate floodplains. The proportion of the landscape at different elevations was determined by lumping point data from a digital elevation model with two-foot contour intervals (Ayres Associates, *unpublished data*) into 3 $\times$ 3 m grid (Table 1). Replicate landscapes were designed using the mean proportion of land at each of the elevations. The replicate landscapes had similar relative abundances of land at different elevations (Table 2). However, the elevations used in the replicate landscapes were adjusted to represent relative elevations, or elevations relative to the channel. The mean proportion of the calibration landscapes occupied by permanent, standing water was determined using ARC/INFO (ESRI 2000) to be 3.1%. For the three most abundant elevation classes, RULE software (Gardner 1999) was used to calculate the fractal dimension (D) of the largest contiguous area at that same elevation or above. D was averaged across these three elevation classes for each calibration landscape. The spatial autocorrelation of the landscapes was measured as the Hurst exponent (H; Saupe 1988). The Hurst exponent is a measure of autocorrelation, ranging from 0 (dispersed) to 1 (very clumped). H was calculated from the fractal dimension (D) where $H = 3 - D$, resulting in a mean $H = 0.055$. The above data were used as input parameters to simulate replicate floodplain landscapes.

Replicate floodplains

The geometry of stream networks and the statistical structure of topography can be characterized by their fractal (or self-similar) properties (Dodds and Rothman 2000). A class of stochastic processes called Fractional-Brownian motions (fBm) exhibit self-affine or fractal-scaling properties and provide realistic representations of certain types of terrain (Goodchild 1988). It had been suggested that patterns produced by fBm are appropriate null models for lake-rich, scale-free landscapes in particular (Goodchild 1988). A fractal distribution may also reasonably represent the distribution of pond size and shape on a floodplain (Fig. 3, see also Hamilton et al. 1992).

Fractal representation of terrain may not be appropriate for all types of topographic relief, however. FBm may be less appropriate null models for eroded or geomorphologically altered terrain formed by processes acting at different scales (Goodchild 1988). Thus, a fBm simulation does not fully represent every aspect of floodplain pond pattern or the forces creating them.

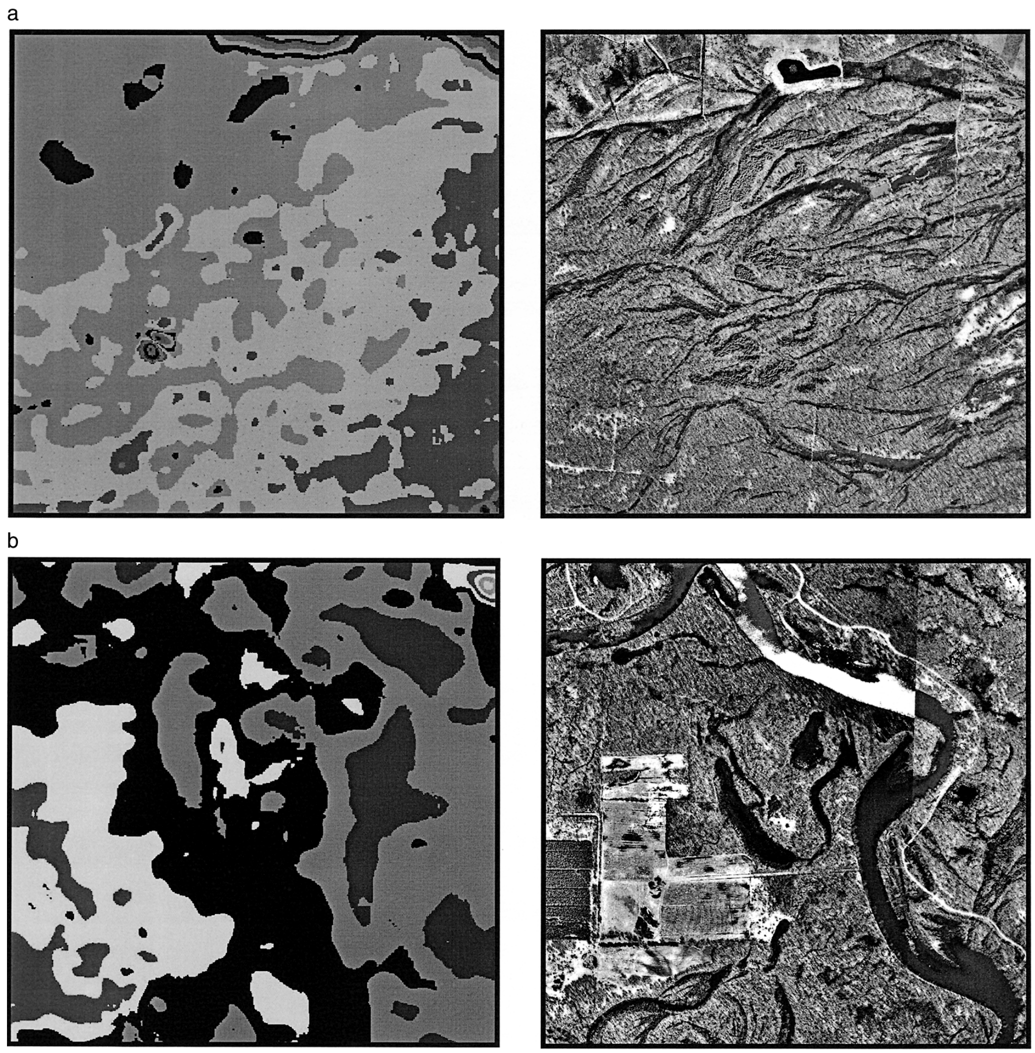

FIG. 2. Two calibration landscapes were used to simulate floodplain topography. Data from these two 1500 × 1500 m areas were used to bound estimates for the proportion of land occupied by different elevation classes, area in permanent standing water, and the spatial autocorrelation (clumpiness) of topography. The panels on the left represent the topographic relief of the areas in 0.5-m intervals; on the right are aerial photos of same areas. (a) Calibration landscape 1; (b) calibration landscape 2.

Furthermore, estimating the fractal dimension can be problematic as the Pareto fit, for example, may not agree with other methods (Kent and Wong 1982, Goodchild 1988, Hamilton et al. 1992). Fractal models have certainly shown some deficiencies in representing terrain (Evans 1998) and it has been suggested that more than five (possibly as many as 12) statistical dimensions are necessary to fully represent terrain variability (Evans 1998). It has even been suggested that attempts to summarize terrain with only one or two parameters is destined to fail (Evans 1998). I argue, however, that such simplifications might certainly be useful for representing certain aspects of the terrain—not all geomorpholgical patterns and processes—but specific features of interest that are relevant to specific problem at hand. The important feature of fBm for this paper is the reproduction of the distribution of pond sizes, for which a fractal model appears reasonable (Fig. 3).

The three features calculated from the calibration landscapes were used in the program RULE (Gardner 1999) to generate the terrain for five replicate multifractal floodplain landscapes (Fig. 4). RULE generates multifractal landscapes using midpoint displacement (Saupe 1988), a commonly used algorithm to create fractal landscapes. This method recursively breaks line segments at their midpoints, then displaces each mid-point a distance proportional to the length of the line segment (Keitt 2000). Each replicate landscape is unique (i.e., initialized by a different random number) and is composed of 3-m pixels covering a 1500

TABLE 1. Percentage of the landscape at different elevations for the two calibration landscapes shown in Fig. 2.

Elevation above sea level (m)	Percentage of landscape: Calibration landscape 1	Calibration landscape 2	Mean	Used in replicate landscapes
237.50–237.99	0.00	0.01	0.01	
238.00–238.49	0.00	10.08	5.04	†
238.50–238.99	0.03	29.47	14.75	†
239.00–239.49	0.04	36.64	18.34	†
239.50–239.99	0.08	18.91	9.50	†
240.00–240.49	0.19	4.68	2.44	†
240.50–240.99	0.41	0.1	0.26	†
241.00–241.49	12.29	0.09	6.19	†
241.50–241.99	40.88	0.03	20.46	†
242.00–242.49	41.83	0.0	20.92	†
242.50–242.99	2.66	0.0	1.33	†
243.00–243.49	0.46	0.0	0.23	‡
243.50–243.99	0.38	0.0	0.19	‡
244.00–244.49	0.29	0.0	0.15	‡
244.50–244.99	0.19	0.0	0.10	
245.00–245.49	0.13	0.0	0.07	
245.50–245.99	0.08	0.0	0.04	
246.00–246.49	0.04	0.0	0.02	
246.50–246.99	0.01	0.0	0.01	
247.00–247.49	0.00	0.0	0.00	

Note: Calibration landscapes were divided into 0.5-m elevation intervals.

† Simulated floodplain landscapes created using the mean percentages, not including elevation categories that occupied ≤0.1% of the landscape.

‡ Mean elevations lumped into one elevation category for the simulated landscapes.

TABLE 2. Input terrain data for simulated, replicate floodplains and corresponding flood stages for flood simulations.

Percentage of landscape	Elevation classes	Flood-recurrence interval: Unregulated flows	Flood-recurrence interval: Regulated flows	Peak flood stage (m)
5.04	242.0			242.0
14.75	242.5		2	242.5
18.34	243.0	2	5	243.0
9.50	243.5	5	25	243.5
2.44	244.0	25	100	244.0
0.26	244.5	100	500	244.5
6.19	245.0	500		245.0
20.46	245.5			245.5
20.92	246.0			246.0
1.33	246.5			246.5
0.57	247.0			247.0

Notes: While the relative percentages of the landscape at different elevations matches the † categories from Table 1, the absolute elevations (relative to sea level) were changed in the simulated floodplains to correspond to elevations relative to river stage. The corresponding discharges are listed in Table 3.

× 1500 m area. The replicate landscapes represent a gradient from low elevation, near the main channel, sloping to areas of higher elevation towards the upland (Fig. 4).

Flood events

Simulated floods were based on the Wisconsin River flood regime, and approximated the timing, flood probabilities, and stage/discharge relationships of the Wis-

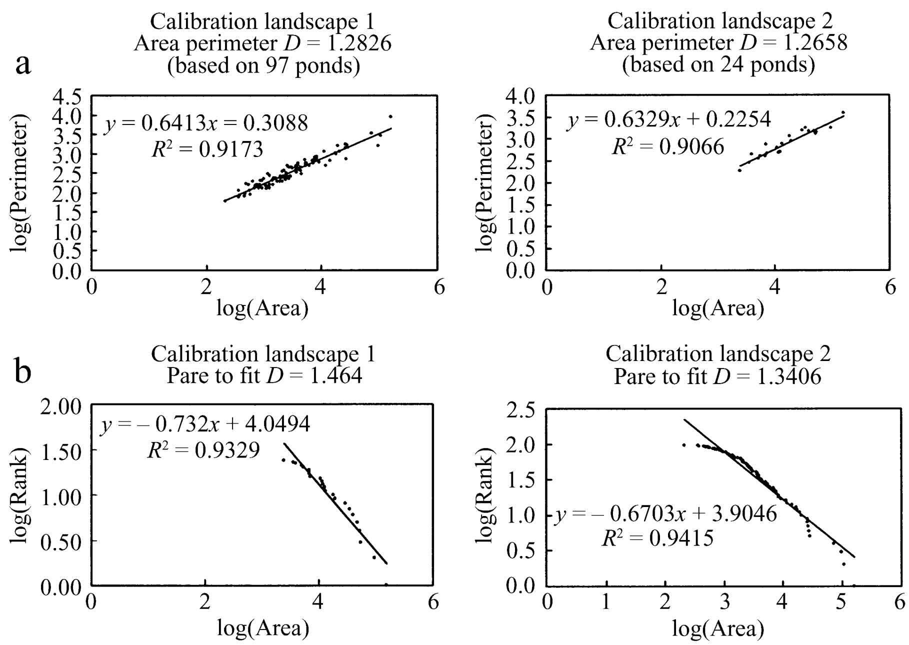

FIG. 3. The shape and the size distribution of permanent ponds [described by the log(area perimeter) and log(rank area) fractal dimension, *D*, respectively] on calibration landscapes suggests that a fractal model of pond distribution is appropriate. (a) Log(area perimeter) fractal dimension for calibration landscape 1 (left) and calibration landscape 2 (right). (b) Log(rank area) fractal dimension for calibration landscapes 1 (left) and 2 (right).

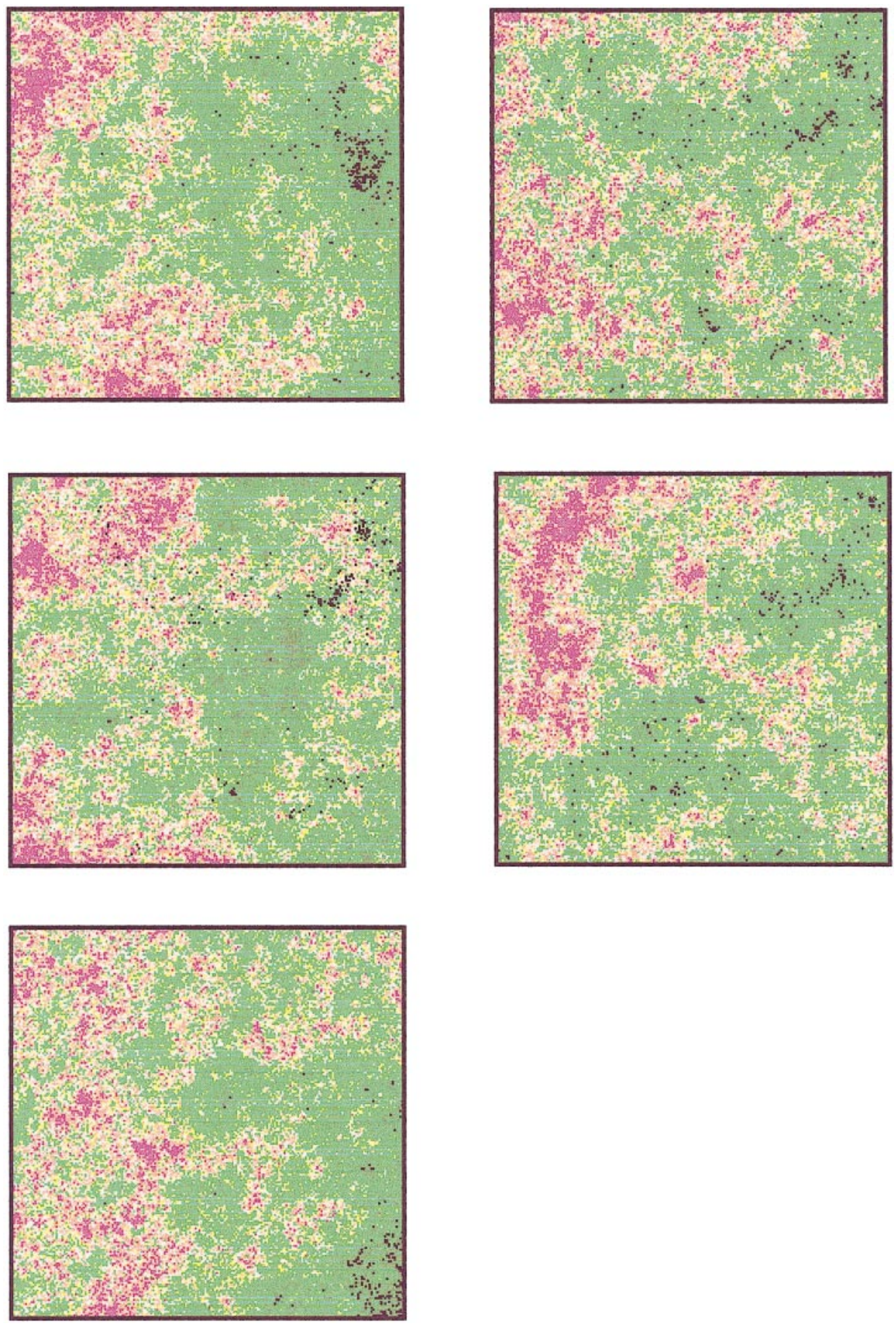

FIG. 4. Topography of the five simulated replicate floodplains (1500 × 1500 m) used in this model. Topographic relief (in 0.5-m intervals) is shown with lower areas in red and higher areas in green. The main channel is located adjacent to the left boundary of each replicate. Note the gradient in topographic relief from the main channel toward the uplands.

consin River below the Wisconsin Dells, Wisconsin. Each simulated flood represented the passing of the flood peak (for one spring flood), set to occur on April 1. Flood probability curves for the Wisconsin River were obtained using PeakFQ software with simulated regulated and unregulated gauge data from Wisconsin Dells (Krug and House 1980). Floods of several different recurrence intervals were modeled (2, 5, 25, 100, 500-yr; Table 3). Using HEC-RAS (Hydrologic Engineering Center—River Analysis System; U.S. Army

TABLE 3. Flood probability estimates for the Wisconsin River at Wisconsin Dells, Wisconsin, under unregulated and regulated (dammed) conditions.

Recurrence interval (yr)	Unregulated discharge (m^3/s)†	Regulated discharge (m^3/s)†
2	1240 (44 000)	950 (33 000)
5	1680 (59 000)	1350 (48 000)
25	2180 (77 000)	1860 (66 000)
100	2490 (88 000)	2220 (79 000)
500	2760 (97 000)	2590 (91 000)

Note: Based on simulated data from Krug and House (1980).

† Discharge in cubic feet per second (cfs) is reported in parentheses.

Corps of Engineers 1998) and accompanying cross-sections for the Wisconsin River, a stage/discharge curve was developed for a cross-section on calibration landscape 1 (see Gergel et al. 2002 for details). When rounded to the nearest 0.5 m, the curve shows an approximately 0.5-m successive incremental increase in stage between each magnitude flood (Table 2). Peak flood stage relative to the elevation of each replicate landscape was used to determine which areas were inundated by a flood. That is, depressions at an elevation equal to or lower than the flood stage were considered inundated. Fig. 5a shows the size distribution of ponds for the natural scenario, for both the 2-yr and a 100-yr magnitude event. Flood patterns for the natural scenario, for both the 2-yr and a 100-yr event illustrate the application of the model (Fig. 5b).

Bates et al. (1998) have developed synthetic fractal floodplains based on real terrain to evaluate and parameterize a hydraulic floodplain model. On such terrain, they examined four stages: (1) bank-full, (2) initial flooding, (3) peak inundation extent, and (4) ponding after the floodwave has passed (Bates et al. 1998). Unlike the Bates et al. (1998) model, the model in this current research presents a phenomenological approach to floodplain inundation, mimicking the pattern of overbank inundation, not unlike the flood patterns left after the passage of the floodwave in Bates et al. (1998). Some topographically isolated ponds are filled during the peak flows, which then subside, leaving discontinuous ponded areas (Fig. 5b). Furthermore, sandy soils with extremely high hydraulic conductivity (such as those along the sandplains of the Wisconsin River) likely allow for significant lateral, shallow subsurface movement of floodwaters. Lastly, some ponds are, in fact, connected by small hydrologic surface connections that are not apparent using even the very fine-scale grid resolution of this model. For example, consider Fig. 2 where the calibration landscapes are shown as aerial photographs as well as gridded elevation maps. It is apparent that many hydrologic surface connections exist on these photographed landscapes that are not identifiable on the gridded representation. All

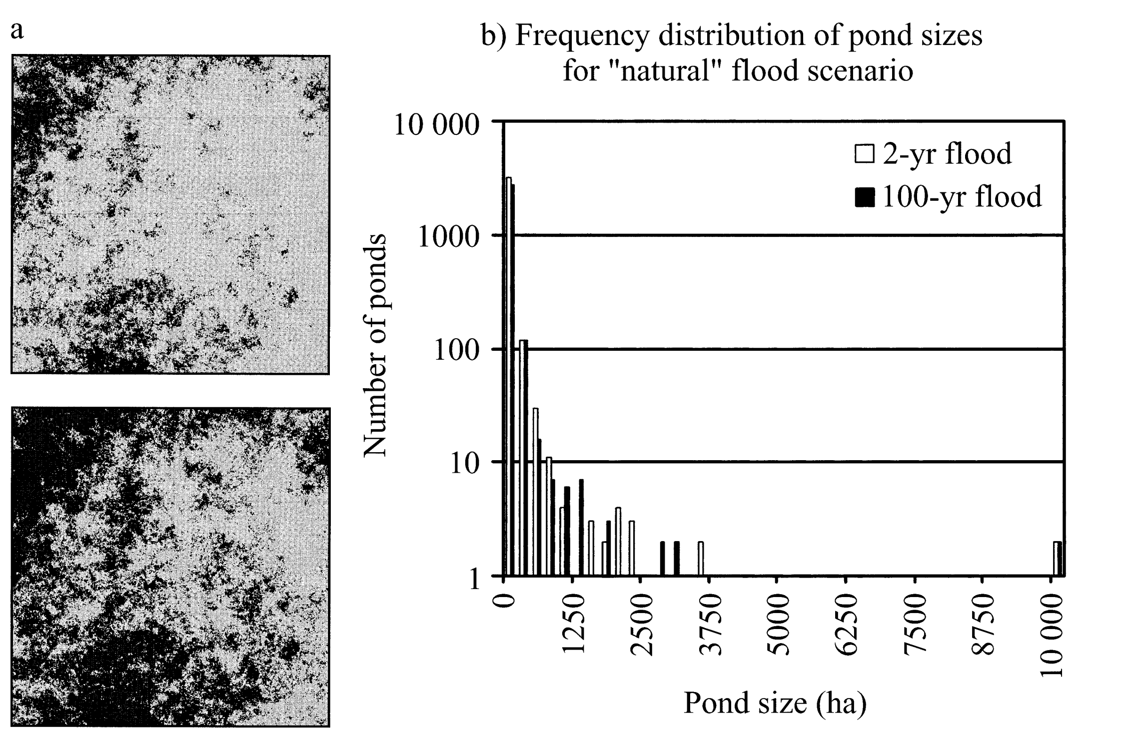

FIG. 5. Example floods of different magnitude on one simulated landscape. (a) Map of ponded area for 2-yr flood (top panel) and 100-yr flood (bottom panel). Black areas are inundated; lighter (gray) areas are not. The density of ponds follows topographic gradient across landscape from lower areas (on left) to higher areas (on right). (b) Size distribution of ponds (of all types) on example flooded landscape for the 2-yr and 100-yr events.

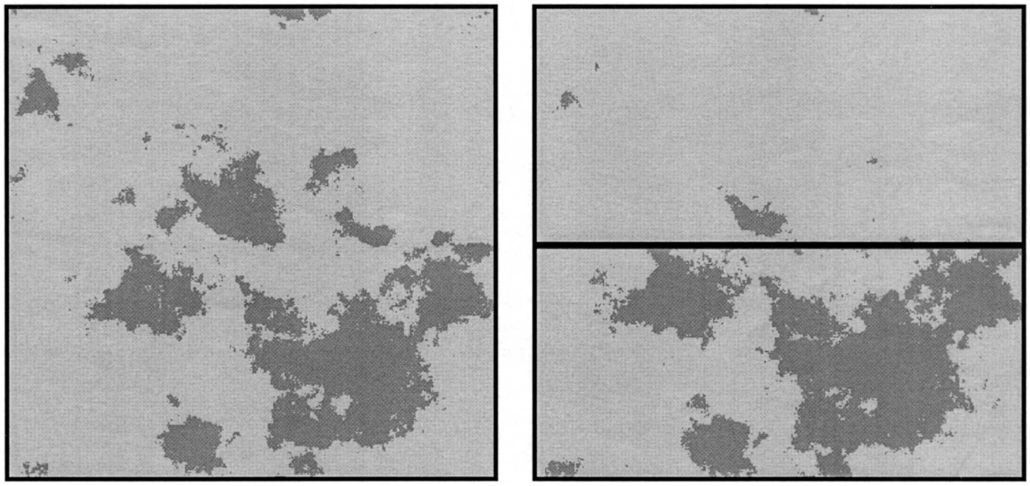

FIG. 6. An example of a simulated flood for a ''natural'' scenario on the left and a ''levee'' scenario on the right. The center line indicates the placement of the levee. Note that, unlike Figs. 4 and 5, the main channel of the river is adjacent to the bottom boundary of each landscape. Dark areas are inundated; lighter areas are not. The levee is not breached in this example, and as such, darker areas on the upland side of levee represent permanent ponds.

of these features suggest that topographically isolated ponds might be capable of filling with inputs from the main channel during flood events.

An upstream dam was simulated using a lower discharge for a given flood probability (Table 1), as caused by the low-head hydroelectric dam at the Wisconsin Dells. For example, the 25-yr event for regulated flow has a lower discharge, and thus lower flood stage, than the unregulated 25-yr flood. Reductions in peak flow are seen downstream of many dams (Williams and Wolman 1984). Levee scenarios were modeled by using the identical floodplain topography as the unleveed scenarios but with a levee structure erected on each landscape (Fig. 6, right-hand panel). The 3-m wide levee is set back from the channel, centered between the channel and the upland edge of the floodplain. Thus, these levee simulations represent the effect of a setback levee, rather than a mainline levee directly adjacent to the channel. The upland side of each levee was not flooded until the levee was overtopped (breached). It is assumed that no seepage occurs below or through the levee. Breaching occurred only for the 100- and 500-yr unregulated floods and the 500-yr regulated (dammed) event. The regulated 100-yr event, of lower stage and discharge, did not breach the levees.

Although not modeled explicitly in this phenomenological approach, the inundation patterns assume a quickly rising hydrograph and a floodwave of short duration. Along the Wisconsin River, the floodwave from overbank inundation moves across the floodplain faster than the floodwave associated with the groundwater table. A longer duration flood dominated by a rising groundwater table would have the potential to fill areas both inside and outside the levee and allow for greater seepage through the levee. Because the effects of the levee are of interest, such types of floods (which would essentially bypass the effect of the levee) are not considered. The interaction between overbank floods and a rising groundwater table would be an important consideration in extrapolating these results to another floodplain, and certainly more mechanistic flood models might be appropriate for understanding other aspects of the flood regime. More mechanism is included in the drainage of the floodplain ponds as an examination of the ecological consequences of pond duration is the goal of this current paper.

The area inundated under each of the four scenarios was calculated and mapped using ARC/INFO. RULE was used to delineate individual ponds (i.e., patches) of contiguous water (Fig. 7). The delineated area of each pond was used in combination with the corresponding elevation data underlying the pond to determine the initial depth and volume of each pond. This information describing individual ponds was exported from ARC/INFO to SAS (SAS Institute 1989) where pond drainage and duration was calculated.

Pond duration

Pond duration was measured on a monthly time step, beginning 1 April and ending 1 September. The duration of each pond was used to classify each pond as permanent (never drying throughout the simulation), semipermanent (drying by 1 August or 1 September), or temporary (drying by 1 June or 1 July). The duration of permanent ponds (assumed to be controlled by groundwater) was not influenced by overbank flooding. Drainage rates for permanent ponds was not calculated as they were permanent by definition and existed before the start of flood simulation. The area of a permanent pond, however, could increase due to inputs from overbank flooding to its basin. Furthermore, once a temporary pond coalesced with a permanent pond, by fill-

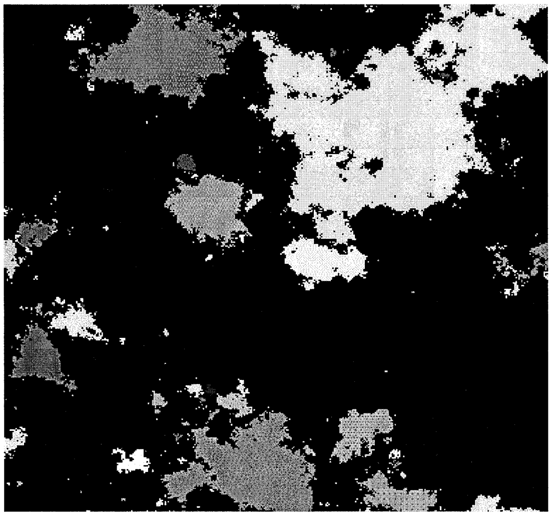

FIG. 7. After a flood event, individual ponds were delineated using RULE software (Gardner 1999). Individual ponds are shown here, each in a unique shade of gray. The surface area and mean depth of each pond were used in determining the volume and duration of each individual pond.

ing deep enough to adjoin an adjacent basin, its hydrologic budget was not calculated further. The entire area occupied by the joined area (now one pond) was considered permanent habitat. Classifying the total conjoined pond area as permanent was indicative of the total area influenced by permanent habitat types and a measure of the area of temporary and semipermanent habitat potentially ''lost'' via coalescing with permanent water bodies. Other depressions in the landscape not connected to permanent water bodies become ephemeral, temporary, or semipermanent ponds receiving water primarily from overbank flooding and precipitation.

The hydrologic budget for the nonpermanent ponds was based on (1) passage of the peak floodwave, (2) precipitation, (3) evaporative losses, and (4) groundwater recharge. Mean monthly precipitation data were obtained from the Midwestern Climate Center. Mean free water surface evaporation (shallow lake) was estimated from mean monthly Class A pan evaporation pan adjusted using a coefficient of 0.78 (Farnsworth et al. 1982). Losses due to groundwater seepage were conceptually similar to that of the River Package subroutine of MODFLOW, a program that simulates seepage between an idealized stream and its groundwater system (McDonald and Harbaugh 1988). We modified the equation to represent pond and groundwater interactions. Groundwater recharge (Q_{out}) was determined as

$$Q_{out} = C_{soil}(H_{pond} - H_{bot})$$

where C_{soil} = soil hydraulic conductivity, H_{pond} = elevation of the top of the pond, and H_{bot} = elevation of the bottom of the pond. The area of the pond that could potentially contribute to evaporative losses and groundwater recharge changed throughout the course of the simulation as the ponds dried and reduced in area. The hydraulic conductivity of unconsolidated deposits of silt can be as low as 1×10^{-9} (Freeze and Cherry 1979). For this model, a value of $C_{soil} = 6 \times 10^{-10}$ was calibrated for moderate-sized flood, assuming a natural (unleveed, undammed) scenario specifically to produce ponds that exhibited a range of hydroperiods across the landscape (from temporary to semipermanent) so that the interactive effects of different modifications could be compared across different pond types. This same soil hydraulic conductivity was then used for all subsequent scenarios.

Statistical analyses

For each replicate landscape, I determined the total ponded area and total number of ponds, as well as the total ponded area and number of ponds of different duration (permanent, semipermanent, and temporary) for each magnitude flood event. I compared the mean number of ponds and the total area of ponded habitat among the four river treatments using a single-factor ANOVA for a given size flood event. Interactive effects of dams and levees were tested using a two $\times$ two factorial design with dams and levees as the cross-factor treatments. A significant interaction term indicated deviation from the additive expectation (Zar 1999). That is, the combined effects were either greater or less than the effects expected by summing the independent effects of dams and the independent effects of levees.

RESULTS

All pond types

In the simulated upstream dam scenario, the total area of ponded habitat decreased by ~10 ha for events smaller than the 100-yr flood as compared to the ''natural'' scenario (Fig. 8a). A setback levee decreased the area of ponded habitat by ~25% for smaller magnitude events, until the levee was breached for the 100- and 500-yr unregulated events. Except for the 2-yr and 500-yr events, an upstream dam increased the total number of all pond types (Fig. 8b). The levee scenarios always showed a decrease in the total number of ponds relative to the natural scenario (by ~30–50%), except when the levees were breached (Fig. 8b).

Permanent ponds

A dam caused a decrease in the area occupied by permanent ponds relative to the ''natural'' scenario for all floods except the 500-yr event (Fig. 9a). The amount of decrease varied greatly by flood magnitude. A levee caused a decrease in the area of permanent ponds by 25% or less, except when the levee was breached in the 100- and 500-yr unregulated floods, where the levee had no effect. The combined effects of both a levee and a dam on pond area were less than additive for the

2-, 5-, and 25-yr events (Fig. 9a), but were synergistic for the 100-yr event.

When considering the number of ponds, a dam increased the number of ponds for the 2-yr event to several times the number of ponds in the natural scenario (Fig. 9b). A levee increased the number of permanent ponds severalfold for the 2- and 5-yr events. Synergistic effects of a dam and a levee together were apparent for the 100-yr event, where the combined effects caused an order of magnitude increase in the number of ponds.

Temporary ponds

A simulated upstream dam had different effects on the area of temporary pond habitat depending on flood magnitude. The area in temporary ponds increased for larger magnitude events (25-, 100-, and 500-yr floods, Fig. 10a), with increases ranging from 1 to 6 ha over the area in the natural scenario. The greatest increase in temporary pond area was for the 500-yr flood (Fig. 10a). For the 2- and 5-yr events, a dam decreased the area of temporary ponds by 4–6 ha as compared to the natural scenario. The mean effect of a levee was to decrease the area occupied by temporary ponds, except for the 100- and 500-yr breaching events when there was no difference between the levee and natural scenarios. Interactive effects were apparent for the 2- and 5-yr events where the combined effect of a levee and a dam was less than might be expected if the effects were additive. Interactive effects between a dam and a levee were also evident for 100-yr flood, where the combined effects on ponded area were synergistic (Fig. 10a).

When considering the total number of ponds, a dam caused an increase for all events except the 2-yr flood, where the mean effect of a dam was to cause a decrease of almost 75% (Fig. 10b). A levee caused a minimum 50% decrease in the number of temporary ponds for the 2-, 5-, and 25-yr (nonbreaching) floods, but had no effect when the levee was breached. Interactive effects of a dam and a levee were apparent for the 2-, 5-, and 100-yr floods. The effects were antagonistic for the smaller events and synergistic for the 100-yr flood.

Semipermanent ponds

Data for the semipermanent ponds are presented primarily for context and help explain discrepancies between the data for all pond types and the summed data for the permanent and temporary ponds (Fig. 11). The most semipermanent ponds and the greatest area in semipermanent ponds occurred with 100- and 500-yr floods. The levee scenario was similar to the natural scenario, whereas a dam caused a large decrease in the number and the area of ponds.

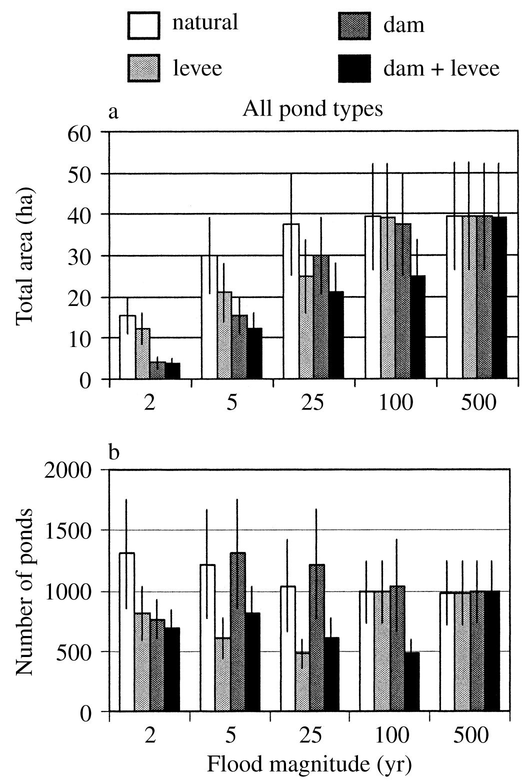

FIG. 8. Mean total ponded area and number of ponds across five simulated replicate landscapes for different magnitude flood events. Each of the five simulated replicate landscapes in Fig. 4 was modeled under four scenarios: natural, dam, levee, and dam + levee for five different magnitude flood events. Error bars are ±1 SE.

DISCUSSION

The influence of an upstream dam on the hydroperiod of simulated floodplain ponds and wetlands was different, but predictable, across different flood magnitudes. Depending on flood magnitude, dams either increased, decreased, or had no effect on the area occupied by temporary pond habitat as compared to the "natural" river scenario. For small floods, a dam decreased the area occupied by temporary ponds. For intermediate magnitude floods, there were no differences, while for the larger magnitude events, regulated flood flows increased the area occupied by temporary ponds. The 5-yr flood with an upstream dam essentially mimicked the flood patterns of the natural 2-yr flood scenario, due to the dampening effect on peak flows. A similar trend was evident when the number of temporary ponds was considered. Changes in the area and number of ponds together provide complementary information about flood patterns. For the 2-yr event, an increase in the number of permanent ponds and a decrease in total area indicates that permanent ponds became smaller and more dispersed. Thus, an upstream dam is likely to reduce connectivity among permanent habitats during small overbank events.

The influence of a simulated levee depended on flood magnitude. The area occupied by different pond types decreased in the levee scenario (relative to the "natural" scenario) except when the levee was breached

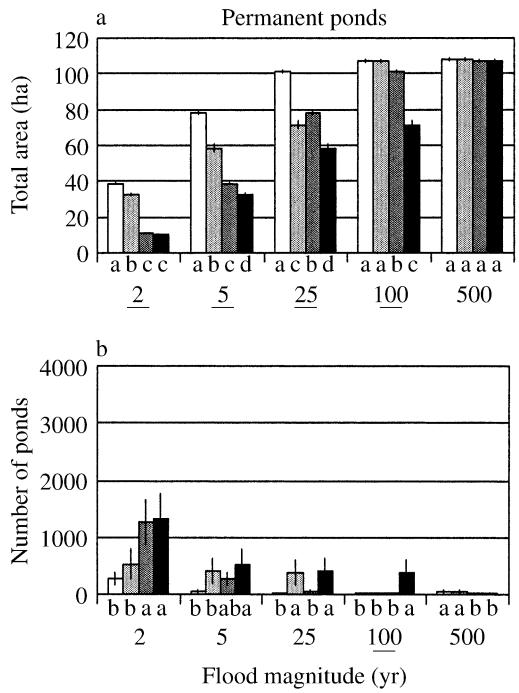

FIG. 9. Mean total area of permanent ponds and number of ponds across five simulated replicate landscapes for different-magnitude flood events. The total area includes temporarily ponded areas that are connected to permanent ponds during the flood. Significant differences between the natural, dam, levee, and dam + levee scenarios are denoted by different letters. Error bars are ±1 SE. An underscore indicates a significant nonadditive interaction between dams and levees in a cross-factor ANOVA for that size flood event. See Fig. 8 for key to scenarios.

during bigger events. However, because I simulated levees set back into the floodplain, the effects of levees were likely underestimated. Greater decreases in area of all pond types would occur if levees were adjacent to the riverbank as the entire floodplain would be cut off from inundation. Second, levees can also produce an increase in stage (flood height) for a given size flood event (Belt 1975), however, I did not model an increase in stage. Increases in flood stage near setback levees along the portion of the Wisconsin River (the area on which this model is based) are on the order of centimeters (Gergel et al. 2002) and below the resolution of this flood model. Implementing an increase in stage in this model would cause (1) an increase in the area of permanent habitats (as ponds on the riverward side of the levee became deeper and more connected) and (2) a decrease in ephemeral habitats (as temporary ponds in the riverward side of levees became subsumed by permanent ponds).

Depending on flood magnitude, the combined effects of levees and dams were either additive, synergistic, or antagonistic. When considering the total area of temporary or permanent ponds, the combined effects of a dam and levee were antagonistic for the smaller magnitude (2- and 5-yr) events. Synergistic effects of both an upstream dam and a levee in combination were evident for the 100-yr flood whether considering the area ponded or the number of ponds, for both permanent and temporary ponds. The synergism results from a reduction in peak flow and stage from the dam. This stage reduction prevents levee breaching for the 100-yr regulated flows, whereas the unregulated 100-yr event would breach the levee. The combined effects of levees and dams on pond area and number were always additive for the 500-yr event because the levees were breached for both the unregulated and regulated flows. In considering other floodplains, the importance of this synergism does not rest with the 100-yr flood, per se, but with the fact that this is the smallest magnitude event capable of breaching the levee. In considering these results within the context of other floodplains it would be necessary to determine whether the area inundated by regulated flows is less than area inundated when leveed, which would depend on the position of the levee and the relative abundance of land at different elevations.

These results are best extrapolated to other floodplains in a qualitative, not a quantitative sense. Next, I present some generalized response curves outlining the effects of an upstream dam and/or a setback levee

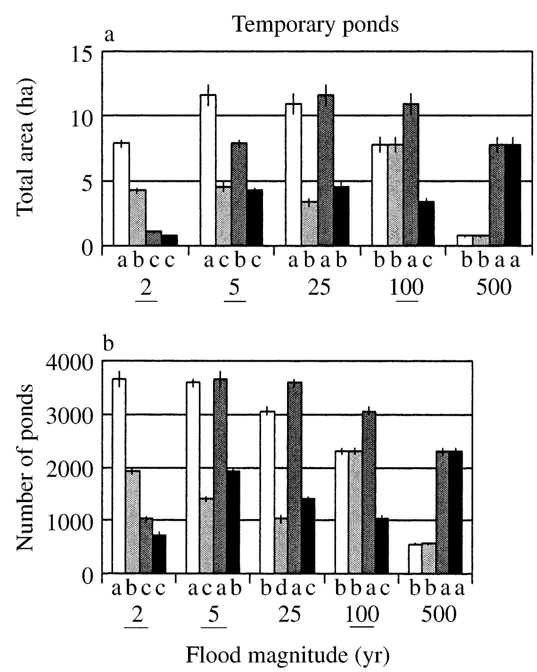

FIG. 10. Mean total area of temporary ponds and number of ponds across five simulated replicate landscapes for different-magnitude flood events. Temporary ponds dry every year, early in the summer (June/July). Significant differences between the natural, dam, levee, and dam + levee scenarios are denoted by different letters. Error bars are ±1 SE. An underscore indicates a significant nonadditive interaction between dams and levees in a cross-factor ANOVA for that size flood event. See Fig. 8 for key to scenarios.

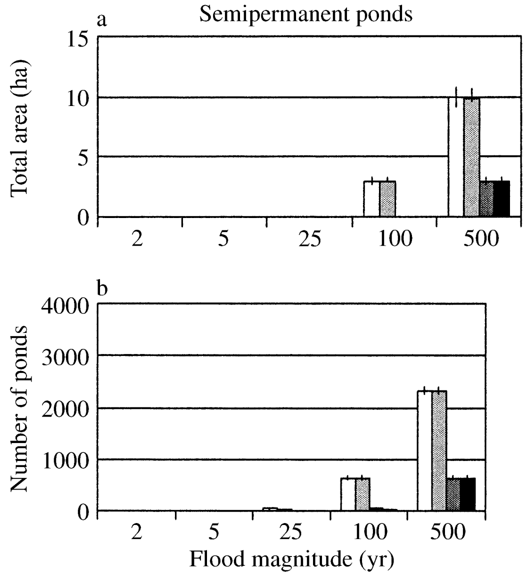

FIG. 11. Mean total area of semipermanent ponds and number of ponds across five simulated replicate landscapes for different magnitude flood events. Semipermanent habitats may not dry every year, and when they do, they typically dry in August. Error bars are ±1 SE. See Fig. 8 for key to scenarios.

on temporary floodplain ponds (Fig. 12). I present these curves as hypotheses for further testing on actual (nonsimulated) floodplains. Generalized response curves for the total area in temporary ponds along rivers with regulated flows as compared to a natural scenario show a decrease in area for small flood events, no difference between the natural and levee scenario at some intermediate flood magnitude, and then an increase for the largest magnitude events (Fig. 12a). A setback levee results in a decrease in the area occupied by temporary ponds, which disappears when the levee is breached (Fig. 12b). An upstream dam and a setback levee (Fig. 12c) had an antagonistic effect for small flood events, and a synergistic response at the breaching threshold for unregulated flows. For any particular floodplain, however, the relative impact of a levee and/or upstream dam would depend on the relative decreases in area flooded caused by a levee or a dam—and this would affect the amount of deviation from the natural scenarios shown on these graphs.

The neutral-terrain model introduced here can address a variety of other spatial questions through manipulating, replicating, and examining floodplain characteristics. For example, what are the consequences of connecting temporary habitats and permanent water bodies during a flood, for water chemistry or for species interactions? In describing the inundation of floodplain lakes along the Orinoco River, Lewis et al. (1990) note that nearby, but separate, basins during the dry season become essentially uniform and contiguous during the flood season. Further, the geomorphic types of back-

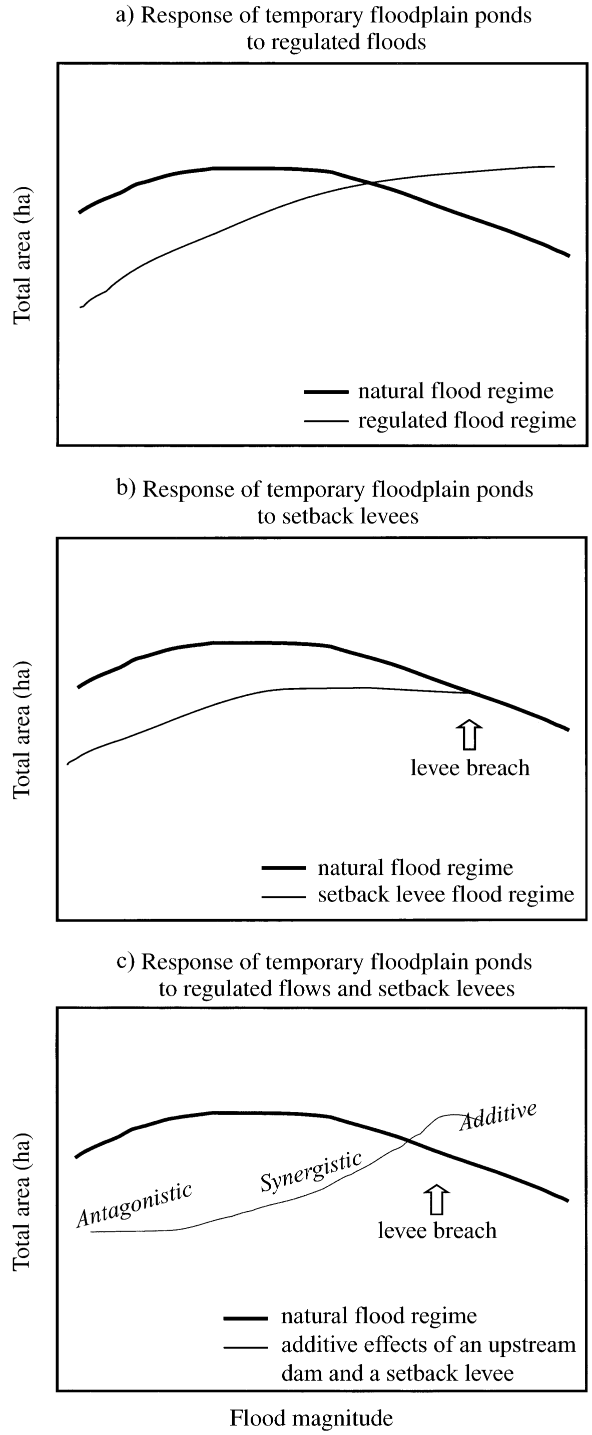

FIG. 12. Conceptual diagram of the effects of (a) an upstream dam and (b) a setback levee on the abundance of temporary floodplain ponds. Panel (c) shows how the non-additive effects of both a dam and a levee on the area of temporary pond habitat change with flood magnitude.

water habitats can be diverse, with varying degrees of connectivity to the main channel (Ward and Stanford 1995) and to each other during overbank floods. Thus, the specific shape of each pond, the distance of ponds from the main channel and backwaters, and the relative positioning among ponds are critical influences on the connectivity of aquatic habitats during a flood pulse. The type of spatially explicit approach presented here is useful to address questions regarding floodplain connectivity.

Furthermore, this neutral-terrain modeling approach can be used in different regions of the world and in different terrain by altering the percentage of land at different elevations and the clumpiness of the topography. The area of any floodplain inundated by a flood would be affected primarily by the amount of land at that same flood-stage elevation. Unlike area, the results for the number of ponds are more directly influenced by the spatial autocorrelation of the topographic relief as this influences the connectivity among different ponds across a flooded landscape. A landscape with highly correlated topography (when considering a spatial lag of one, or the nearest neighbor) would result in fewer, larger, more connected ponds; whereas a landscape with more dissected topography would result in more ponds of smaller mean size, dispersed throughout the landscape.

Simulated floodplain topography is also needed specifically to aid in the calibration of more complicated two-dimensional hydraulic floodplain models that are continually being developed and improved (Bates et al. 1998, Tchamen and Kahawita 1998). The refinement of such models that predict spatially distributed variables (e.g., velocity, depth, and inundation extent) has been hampered by a lack of suitable topographic data (Bates et al. 1998). Data sets capable of validating high resolution flow models often do not exist or may contain inaccurate and insufficient topographic data as well as considerable measurement errors (Bates et al. 1998, Marks and Bates 2000). Available topographic data are often not commensurate with the potential abilities of newly developing two-dimensional finite element models (Marks and Bates 2000). Simulated terrain can be extremely valuable for the further development of such models (Bates et al. 1998). With the exception of fractals (Rodriguez-Iturbe and Rinaldo 1997, Bates et al. 1998), there has not been an exceptional amount of research on synthetic topography (Evans 1998, Bates et al. 1998), and thus, neutral-terrain modeling techniques have the potential to rapidly improve. Furthermore, when combined with innovative remote sensing techniques of floodplains and overbank events (Alsdorf et al. 2000, Benke et al. 2000) such applications will help drastically improve our ability to understand and model (as well as verify our models) of the spatial dynamics of flooding. Ecologists should take advantage of these interdisciplinary advances to further our understanding of the ecological impacts of flooding and altered flood regimes.

Lastly, while there are many case studies of multiple disturbances (Paine et al. 1998), those involving wetlands have emphasized cumulative impacts (Bedford and Preston 1988, Abbruzzese and Leibowitz 1997). The President's Council on Environmental Quality defined cumulative impacts to include the impacts of ''past, present, and reasonable foreseeable future actions'' (McCold and Saulsbury 1996). Certainly considering the interaction of more than one disturbance is important for river and wetland restoration projects. For example, restoring a wetland on the upland side of a levee that was previously drained for agriculture would be difficult, as the levee restricts the natural overbank flooding (Abbruzzese and Leibowitz 1997). Multiple disturbances to wetlands can have collectively different effects than the sum of individual alterations (Gosselink et al. 1990, Spaling and Smit 1993). However, explicit testing for synergistic and antagonistic effects of multiple disturbances have largely remained divorced from the studies of cumulative impacts to wetlands. Certainly much could be gained by merging the practical goals of cumulative impact analysis with the theoretical techniques for quantifying the interactions of disturbances (such as factorial designs of multiple disturbances and/or the use of simulation experiments). Furthermore, because the hydroperiod of a specific wetland is based on such a variety of factors, the hydrologic pattern of wetlands may be a useful indicator for which cumulative impacts can be identified, interpreted and assessed (Nestler and Long 1997).

Understanding the role of compound disturbances, both natural and anthropogenic, will be fundamental to environmental decisions making in the twenty-first century (Paine et al. 1998). In the case of large rivers, there is a growing need to understand and predict their ecological response to massive human alterations (Power et al. 1995). Undoubtedly this will involve the consideration of multiple disturbances, including not only levees and dams, but also wetland drainage, conversion to agricultural, roads and increasing urbanization in watersheds. Neutral-terrain modeling presents an important new approach for examining concurrent disturbances that occur within a broad spatial context.

Acknowledgments

This work has been inspired by conversations with, and the work of many individuals. Monica Turner, and the work of Robert Gardner (and his program RULE) help lay the foundation for my ideas on the use of neutral landscape models. Jon Chase has helped engender context and new uses for this neutral-terrain modeling approach in aquatic systems. Roy Plotnick provided advice on measuring spatial autocorrelation in real terrain. Conversations with Emily Stanley and Randy Hunt were absolutely critical in understanding flooding on the Wisconsin River and its floodplain and general advice on floodplain geomorphology from John Melack was extremely helpful. Lastly, the exciting environment of University of Wisconsin–Madison, particularly the Center for Limnology, provided an ideal setting for the development of a model linking the concepts of aquatic and landscape ecology. Joy Zedler deserves special thanks for her extremely detailed, thoughtful comments on this work. Her editorial suggestions have improved every page of this manuscript. The comments of two anonymous reviewers greatly improved the clarity of this manuscript. Many thanks go to the Sand County Foundation, Brent Haglund, and Ayres Associates as nearly all of the spatial data for the study area of the Wisconsin River were developed and graciously provided by them. This work was funded by an NSF Graduate Traineeship in Limnology and an EPA STAR Fellowship.

Literature Cited

Abbruzzese, B., and S. G. Leibowitz. 1997. A synoptic approach for assessing the cumulative impacts to wetlands. Environmental Management **21**(3):457–475.

Alsdorf, D. E., J. M. Melack, T. Dunne, L. A. K. Mertes, L. L. Hess, and L. C. Smith. 2000. Interferometric radar measurements of water level changes on the Amazon floodplain. Nature **404**:174–177.

Bates, P. D., M. Horritt, and J.-M. Hervouet. 1998. Investigating two-dimensional, finite element predictions of floodplain inundation using fractal generated topography. Hydrological Processes **12**:1257–1277.

Bedford, B. L., and E. M. Preston, editors. 1988. Cumulative effects on landscape systems of wetlands: scientific status, prospects and regulatory perspectives. Environmental Management **12**(5):561–775.

Belt, C. B., Jr. 1975. The 1973 flood and man's constriction of the Mississippi River. Science **189**:681–684.

Benke, A. C., I. Chaubey, G. M. Ward, and E. L. Dunn. 2000. Flood pulse dynamics of an unregulated river floodplains in the southeastern U.S. coastal plain. Ecology **81**:2730–2741.

Breitburg, D., S. Seitzinger, and J. Sanders, guest editors. 1999. The effects of multiple stressors on freshwater and marine ecosystems. Special Issue of Limnology and Oceanography **44**:739–972.

Brinson, M. 1993. Changes in the functioning of wetlands along environmental gradients. Wetlands **13**:65–74.

Casanova, M. T., and M. A. Brock. 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? Plant Ecology **147**(2): 237–250.

Corti, D., S. L. Kohler, and R. E. Sparks. 1997. Effects of hydroperiod and predation on a Mississippi River floodplain invertebrate community. Oecologia **109**(1):154–165.

Dodd, C. K. 1992. Biological diversity of a temporary pond herpeto fauna in North Florida sandhills. Biodiversity and Conservation **1**(3):125–142.

Dodds, P. S., and D. H. Rothman. 2000. Scaling, universality and geomorphology. Annual Review of Earth and Planetary Sciences **28**:571–610.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science **266**:753–762.

ESRI. 2000. Understanding GIS: the ARC/INFO method. Environmental Systems Research Institute, Redlands, California, USA.

Evans, I. S. 1998. What do terrain statistics really mean? Pages 119–138 *in* S. Lane, K. Richards, and J. Chandler, editors. Landform monitoring, modeling and terrain analysis. John Wiley and Sons, New York, New York, USA.

Farnsworth, R. K., E. S. Thompson, and E. L. Peck. 1982. Evaporation atlas for the contiguous 48 United States. NOAA Technical Report NWS 33. National Weather Service, Washington, D.C., USA.

Fitzpatrick, F. A., J. C. Knox, and H. E. Whitman. 1999. Effects of historical land-cover changes on flooding and sedimentation, North Fish Creek, Wisconsin. U.S. Geological Survey Water Resources Investigations Report 99-4083.

Freeze, R. A., and J. A. Cherry. 1979. Groundwater. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Gardner, R. H. 1999. RULE: map generation and spatial analysis program. Pages 280–303 *in* J. M. Klopatek and R. H. Gardner, editors. Landscape ecological analysis: issues and applications. Springer-Verlag, New York, New York, USA.

Gardner, R. H., B. T. Milne, M. G. Turner, and R. V. O'Neill. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecology **1**:19–28.

Gergel, S. E., M. D. Dixon, and M. G. Turner. 2002. Consequences of human-altered floods: levees, floods, and floodplain forests along the Wisconsin River. Ecological Applications **12**:1755–1770.

Goodchild, M. F. 1988. Lakes on fractal surfaces: a null hypothesis for lake-rich landscapes. Mathematical Geology **20**(6):615–630.

Gosselink, J. G., G. P. Shaffer, and L. C. Lee. 1990. Landscape conservation in a forested wetland watershed—can we manage cumulative impacts? BioScience **40**:588–600.

Hamilton, S. K., J. M. Melack, M. F. Goodchild, and W. M. Lewis. 1992. Estimating the fractal dimension of terrain from lake size distributions. Pages 145–163 *in* P. A. Carling and G. E. Petts, editors. Lowland floodplain rivers: geomorphological perspectives. John Wiley and Sons, New York, New York, USA.

Holling, C. S., and S. Sanderson. 1996. Dynamics of (dis)harmony in ecological and social systems. Pages 57–58 *in* S. S Hanna, C. Folke, and C. G. Maler, editors. Rights to nature. Island Press, Washington, D.C., USA.

Johnston Associates. 1989. A status report on the nation's floodplain management activity: an interim report prepared for Interagency Task Force on Floodplain Management. U.S. Government Printing Office, Washington, D.C., USA.

Keitt, T. H. 2000. Spectral representation of neutral landscapes. Landscape Ecology **15**:479–493.

Kent, C., and J. Wong. 1982. An index of littoral zone complexity and its measurement. Canadian Journal of Fisheries and Aquatic Sciences **39**:847–853.

Krug, W. R., and L. B. House. 1980. Streamflow model of Wisconsin River for estimating flood frequency and volume. Water-resources investigations, open file report 80-1103. U.S. Geological Survey in cooperation with the Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

Leeper, D. A., and B. E. Taylor. 1998. Abundance, biomass, and production of aquatic invertebrates in Rainbow Bay, a temporary wetland in South Carolina, USA. Archiv for Hydrobiologie **143**(3):335–362.

Lewis, W. M., Jr., F. H. Weibezahn, J. F. Saunders, and S. Hamilton. 1990. The Orinoco as an ecological system. Interciencia **15**:346–357.

Marks, K., and P. Bates. 2000. Integration of high-resolution topographic data with floodplain flow models. Hydrological Processes **14**:2109–2122.

McCold, L. M., and J. W. Saulsbury. 1996. Including past and present impacts in cumulative impact assessments. Environmental Management **20**:767–776.

McDonald, M. G., and A. W. Harbaugh. 1988. Techniques of water resources investigations of the United States Geological Survey. Book 6: modeling techniques. Chapter A1: a modular three-dimensional finite-difference ground-water flow model. Unites States Government Printing Office, Washington, D.C., USA.

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands. Van-Nostrand Reinhold, New York, New York, USA.

Murkin, H. R., E. J. Murkin, and J. P. Ball. 1997. Avian habitat selection and prairie wetland dynamics: a 10-year experiment. Ecological Applications **7**:114–1159.

Nestler, J. M., and K. S. Long. 1997. Development of hydrological indices to aid cumulative impact analysis of riverine wetlands. Regulated Rivers: Research and Management **13**:317–334.
Nilsson, C., R. Jannson, and U. Zinko. 1997. Long-term responses of river-margin vegetation to water-level regulation. Science **276**:798–800.
Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1**:535–545.
Petts, G. E. 1989. Perspectives for ecological management of regulated rivers. Pages 3–26 *in* J. A. Gore and G. E. Petts, editors. Alternatives in regulated river management. CRC, Boca Raton, Florida, USA.
Potter, K. W. 1991. Hydrological impacts of changing land management practices in a moderate-sized agricultural catchment. Water Resources Research **27**:845–855.
Potter, K. W. 1994. Estimating potential flood reduction benefits of restored wetlands. Update: Water Resources, The University Council on Water Resources **97**:34–36.
Power, M. E., A. Sun, G. Parker, W. E. Dietrich, and J. T. Wooten. 1995. Hydraulic food-chain models. BioScience **45**:159–167.
Rodriguez-Iturbe, I., and A. Rinaldo. 1997. Fractal river basins: chance and self-organization. Cambridge University Press, Cambridge, UK.
SAS Institute. 1989. SAS/STAT user's guide. Version 6. Fourth edition. Volume 1. SAS Institute, Cary, North Carolina, USA.
Saupe, D. 1988. Algorithms for the random fractals. Pages 71–113 *in* H. O. Petigen and D. Saupe, editors. The science of fractal images. Springer-Verlag, New York, New York, USA.
Schindler, D. W., P. J. Curtis, B. R. Parker, and M. P. Stainton. 1996. Consequences of climate warming and lake acidification for UV-B penetration in North American boreal lakes. Nature **379**:705–708.
Schneider, D. W., and T. M. Frost. 1996. Habitat duration and community structure in temporary ponds. Journal of the North American Benthological Society **15**(1):64–68.
Skelly, D. K., E. E. Werner, and S. A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology **80**:2326–2337.
Snodgrass, J. W., J. W. Ackerman, A. L. Bryan, and J. Burger. 1999. Influence of hydroperiod, isolation, and heterospecifics on the distribution of aquatic salamanders (siren and amphiuma) among depression wetlands. Copeia 1:107–113.
Snodgrass, J. W., C. H. Jagoe, A. L. Bryan, H. A. Brant, and J. Burger. 2000*a*. Effects of trophic status and wetland morphology, hydroperiod, and water chemistry on mercury concentrations in fish. Canadian Journal of Fisheries and Aquatic Sciences **57**(1):171–180.
Snodgrass, J. W., M. J. Komorski, A. L. Bryan, and J. Burger. 2000*b*. Relationships among isolated wetland size, hydroperiod and amphibian species richness: implications for wetland regulations. Conservation Biology **14**(2):414–419.
Spaling, H., and B. Smit. 1993. Cumulative environmental change: conceptual frameworks, evaluation approaches and institutional perspectives. Environmental Management **17**(5):587–600.
Sparks, R. E. 1995. Need for ecosystem management of large rivers and their floodplains. BioScience **45**(3):168–182.
Tchamen, G. W., and R. A. Kahawita. 1998. Modeling wetting and drying effects over complex topography. Hydrological Processes **12**:1151–1182.
Tobin, G. A. 1995. The levee love affair: a stormy relationship. Water Resources Bulletin **31**(3):359–367.
U.S. Army Corps of Engineers (USACE). 1998. HEC-RAS river analysis system, user's manual. Version 2.2. U.S. Army Corps of engineers, Hydrologic Engineering Center. Davis, California, USA.
Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of earth's ecosystems. Science **277**:494–499.
Ward, J. V., and J. A. Stanford. 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated River: Research and Management **11**: 105–119.
Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics **27**:337–363.
Werner, E. E., and M. A. McPeek. 1994. Direct and indirect effects of predators on 2 anuran species along an environmental gradient. Ecology **75**:1368–1382.
Williams, D. D. 1997. Temporary ponds and their invertebrate communities. Aquatic Conservation—Marine and Freshwater Ecosystems **7**(2):105–117.
Williams, G. P., and M. G. Wolman. 1984. Downstream effects of dams on alluvial rivers. Geological Survey Paper 1286. United States Government Printing Office, Washington, D.C., USA.
Wissinger, S. A., H. H. Whiteman, G. B. Sparks, G. L. Rouse, and W. S. Brown. 1999. Foraging trade-offs along a predator-permanence gradient in subalpine wetlands. Ecology **80**:2102–2116.
With, K. A., and A. W. King. 1997. The use and misuse of neutral landscape models in ecology. Oikos **79**:219–229.
Yan, N. D., W. Keller, N. M. Scully, D. R. S. Lean, and P. J. Dillon. 1996. Increased UV-B penetration in a lake owing to drought-induced acidification. Nature **381**:141–143.
Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, New Jersey, USA.