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ENVIRONMENTAL PERSISTENCE AND THE STRUCTURE/COMPOSITION OF NORTHERN PRAIRIE MARSHES

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Abstract: Fractal time-series analysis (Hurst range scaling) and temporal autocorrelation were used to examine the persistence of water level fluctuations in the Delta Marsh, Canada. Persistence was quantified by calculating the Hurst fractal exponent (H) for two time periods. The period from 1924-1960 was used to determine persistence prior to the installation of the Fairford water control structure in 1961. The period 1962-1996 was also examined, to determine how human regulation of water levels since 1961 has affected system persistence. Prior to 1961, water level fluctuations displayed high persistence ($H = 0.844$). However, persistence has declined ($H = 0.737$) since water level regulation began in 1961. The importance of environmental (water level) persistence in controlling the community structure, dynamics, and species composition of Delta Marsh and other northern prairie marshes is discussed. It is suggested that decreased persistence may be as important as a decline in the magnitude of water fluctuations in explaining changes in vegetation composition and structure that have occurred in the Delta Marsh since 1961. Higher environmental persistence appears to promote species-habitat diversity and productivity in northern prairie marshes.

Introduction

The 21,870 ha Delta Marsh occurs along the south shore of Lake Manitoba, Canada (50°10'N, 98°19'W), and is one of largest remaining natural marshes on the North American prairie. It is directly connected to Lake Manitoba by a series of channels crossing a forested, sandy barrier ridge. Dominant emergent macrophyte species in the marsh include the bulrushes (*Scirpus* spp.), cattails (mainly the hybrid *Typha glauca*), reed grass (*Phragmites australis*), whitetop grass (*Scholochloa festucacea*), and the sedge *Carex atherodes* (refer to Löve & Löve (1954) for a complete description of the vegetation).

North American prairie marshes are dynamic ecosystems that undergo changes in vegetation composition and structure in response to cyclically fluctuating water levels (van der Valk 1981). Many of the emergent macrophyte beds that dominate the marsh are killed during sustained periods of high water. Once water levels fall again, the exposed mudflats are initially colonized by ruderal, opportunistic plants such as *Chenopodium rubrum*, and later by emergent species (Walker 1965). Fluctuating water levels play a key role in this dynamic process of marsh rejuvenation, promoting and maintaining high levels of species richness and habitat diversity (van der Valk 1981).

Since 1961, water levels in Lake Manitoba and the Delta Marsh have been regulated by a dam on the Fairford River, Lake Manitoba's only outlet. This control structure was installed following severe flooding in 1955, when the lake reached 248.7 m a.s.l. (ca. 1.7 m higher than the level only 12 years earlier). Very high water levels in 1955, coupled with strong winds and wave action, caused extensive flooding in Delta Marsh and adjacent farmland (Olsen 1959). This prolonged flood killed much of the emergent macrophyte vegetation in Delta Marsh, but the system quickly recovered once water levels fell (Walker 1965).

The control structure at Fairford has reduced the magnitude of water level fluctuations in Lake Manitoba and Delta Marsh. Prior to 1961, water levels fluctuated widely and regularly, but since 1961 fluctuations have rarely exceeded 50 cm. It has been hypothesized that disruption of the natural cycle of water level fluctuations has prevented marsh rejuvenation from occurring; the marsh has entered a 'lake-marsh' phase (van der Valk 1981) of lessened productivity and lowered species-habitat diversity. De Gues (1987) examined aerial photographs over five time periods (1948, 1954, 1964, 1972 and 1980) to determine changes in vegetation composition in 41 one ha plots in the Delta Marsh. Her main finding was that shorelines of the pre-regulation marsh (before 1961) were dominated by reed grass, whereas post-regulation shorelines have been increasingly colonized by hybrid cattail. Considerable encroachment of cattail into stands of reed grass and shallow open-water areas was also noted. Since 1961, declines in the cover-abundance of bulrush species, and in muskrat and marsh bird populations, have also occurred.

While changes in the vegetation structure and species composition of Delta Marsh since 1961 have been attributed to water level regulation, a detailed analysis of water level variation prior to and after 1961 has never been undertaken.

A time-series analysis of these data is necessary to quantify changes that have occurred in the temporal dynamics of water level fluctuations since 1961. Such an analysis may help to explain observed changes in vegetation composition and structure than have occurred over the past 35 years.

Hurst (1951) pioneered a time-series approach to the analysis of river discharges and other geophysical series. Today his work is recognized as an early example of the study of natural fractal geometry (Mandelbrot 1982). Hurst used his 'range rescaling' method to determine the size of the storage reservoir required to contain Nile River floodwaters. Range rescaling quantifies the degree of 'persistence' in a temporal series (Schroeder 1991), which is defined as "the temporal grouping of nonperiodic, similar events" (Outcalt et al. 1997). The statistic used is the Hurst exponent H, which ranges from 0 to 1. Nile River discharges display high persistence ($H = 0.91$), whereas comparatively "mild and tame" rivers such as the Rhine have comparatively low persistence, $H = 0.55$ (Schroeder 1991).

The concept of persistence, and consequences on natural systems and processes, are best illustrated by considering possible time-series traces. Schroeder (1991: 121) conveniently classifies time-series traces in terms of 'noise'. White noise is defined when successive values in a series are completely uncorrelated. The power spectrum of white noise is independent of frequency, implying that the system lacks memory or 'persistence'. White noise can be easily generated by plotting a series of independent random numbers against time.

Formally, the integral of white noise produces a trace known as 'brown noise' (Voss 1988). This is also known as a Brownian or 'random walk' trace, since it represents the projection of Brownian motion onto a single dimension. Brown noise is a convenient null model when analyzing biogeophysical time series, as it represents the expected trace under a hypothesis of random temporal variation. Brown noise displays short-term persistence (i.e. long-term temporal correlations are absent), the result of chaotic effects attributable to the weak information storage capacity of a system. The power spectrum of brown noise is proportional to the inverse of the squared frequency (Voss 1988). Brown noise can be generated by plotting the cumulative sum of independent random numbers of zero mean against time (Schroeder 1991; Hastings & Sugihara 1993).

For a given time series, the expected change in a value V, $\Delta V = V(t_2)-V(t_1)$, for the time interval $\Delta t = t_2 - t_1$ can be expressed using the scaling law relationship:

$$\Delta V \propto \Delta t^H \qquad (1)$$

where H is the Hurst exponent (Voss 1988). For white noise, $H = -0.5$. Brown noise has an expected value of $H = 0.5$, implying that displacement in a random walk consisting of n steps scales as $n^{0.5}$. Natural geophysical time series typically have values of $H > 0.5$, usually ranging from $H = 0.6 - 0.9$ (Outcalt et al. 1997). Time-series traces for which $H > 0.5$ are termed 'black noise' (Schroeder 1991). Such series exhibit non-random behaviour, with higher values of H reflecting greater long-term memory or persistence in the system. The power spectrum of black noise is proportional to $f^{-\beta}$, where $\beta > 2$. Mandelbrot & van Ness (1968) describe a class of self-similar processes, known as fractional Brownian noise (fBn), that display 'infinite memory' ($0.5 \leq H \leq 1.0$). Such processes, which are characterized by long-term correlation or persistence, have been widely used to describe and model geophysical time series (Outcalt et al. 1997).

In this paper, I perform fractal-based (Hurst range rescaling) times series analyses on Lake Manitoba water levels. The objective is to compare and contrast trends prior to (1924–1960) and following (1962–1996) water level regulation. I then relate changes in water level dynamics (persistence) since 1961 to observed changes in the vegetation composition and community structure of Delta Marsh.

Materials and Methods

The analyses used mean monthly water level (m a.s.l.) data from Lake Manitoba for the years 1924–1996 (73 years, $n = 876$). The data were subdivided into two time periods: (a) prior to water level regulation, 1924-1960 (37 years, $n = 444$); (b) following water level regulation, 1962–1996 (35 years, $n = 420$). Hurst range rescaling (explained below) was applied to the entire data set, and to each of the two sub-periods. The data were also analyzed using yearly rather than monthly means. Temporal autocorrelation (explained below) was also used to examine monthly trends in the pre- and post-control data sets.

Hurst Range Rescaling

Hurst range rescaling is a time series transformation that produces a measure of divergence for characterizing 'black noise' processes. The transformation amounts to computing cumulative deviations from the series mean, and determining the range of this rescaled series. The Hurst exponent H, a measure of persistence, is computed simply as:

$$H = (\log [R_n/S_n]) \,/\, (\log n) \qquad (2)$$

where R_n and S_n are, respectively, the range of cumulative departures from the mean and the standard deviation for a time series of length n (Schroeder 1991: 130). Outcalt et al. (1997) provide a detailed worked example, and demonstrate how a graph of the normalized rescaled range can be used to summarize trends in temporal persistence.

The Hurst exponent H quantifies the dependence or persistence of a 'black noise' series. Higher persistence (larger H) implies that an increasing trend will tend to continue to increase (or conversely, that a decreasing trend will continue to decrease). Temporal series of high H have comparatively 'smooth' traces, implying strong temporal autocorrelation and long-term persistence (Voss 1988). The relationship between H and the power spectrum exponent ($f^{-\beta}$) is given by $\beta = 2H + 1$ (Schroeder 1991), while the fractal dimension is simply $D = 2 - H$ (Voss 1988:45).

Temporal Autocorrelation

Autocorrelation is simply the sequential or serial correlation of a temporal series (Legendre & Legendre 1983). The autocorrelation for a temporal lag of length k is:

$$r_k = \mathrm{COV}(X_t, X_{t+k}) / \sqrt{[\mathrm{VAR}(X_t)\,\mathrm{VAR}(X_{t+k})]} \quad (3)$$

where X_t and X_{t+k} are values in the series, COV is the covariance, and VAR is the variance. A plot of autocorrelation as a function of lag length, known as a correlogram, summarizes the nature and relative 'strength' of temporal autocorrelation in a series.

Results

Water Level Fluctuations, 1924-1996

Mean monthly water levels for Lake Manitoba (Steep Rock Station No. 05LK002) for the period 1924-1996 are summarized in Fig. 1. Mean water levels (± 1 s.d.) are 247.51 ± 0.27 m a.s.l. for the entire 73 year period, and 247.55 ± 0.36 m and 247.46 ± 0.12 m for the periods 1924-1960 and 1962-1996, respectively. The range in water levels was 1.71 m prior to 1961, and 0.83 m since 1961. These results indicate that regulation has indeed 'stabilized' lake levels. However, these univariate statistics do not consider the temporal dynamics (autocorrelation) of the data.

Temporal Autocorrelation

Temporal correlograms for the pre-regulation (1924-1960) and post-regulation (1962-1996) periods are presented in Fig. 2. Strong differences in temporal autocorrelation are apparent. For the pre-regulation data, temporal autocorrelation is strong and declines monotonically with lag period. Autocorrelation is positive and statistically significant up to a four-year lag period, while lag periods of 12 years or more are negatively autocorrelated. Temporal autocorrelation of water levels is much weaker for the post-regulation data, and the dominant trend reflects annual fluctuations. Even so, the autocorrelation of annual water levels (lag period of one year) is much stronger prior to 1961 (r = 0.85) than since 1961 (r = 0.49). These results indicate that regulation of Lake Manitoba water levels has resulted in fluctuations that are far less predictable over time, in both the short and long term.

Hurst Range Rescaling

Using the monthly mean data, the Hurst exponent for the period 1924-1996 was H = 0.776, while values of H = 0.844 and H = 0.737 were obtained for the 1924-1960 and 1962-1996 periods, respectively. Using yearly means, the corresponding values were H = 0.656 (1924-1996), H = 0.738 (1924-1960) and H = 0.622 (1962-1996). The higher values obtained using the monthly data are likely attributable to strong intra-annual autocorrelation. The results indicate that persistence, as measured by H, has declined substantially since water level regulation began in 1961. This is also apparent from the plot of normalized range rescales values for the period 1924-1996 (Fig. 3). In interpreting the normalized plot, a descending trace indicates persistence of values less than the long-term mean water level, while an ascending

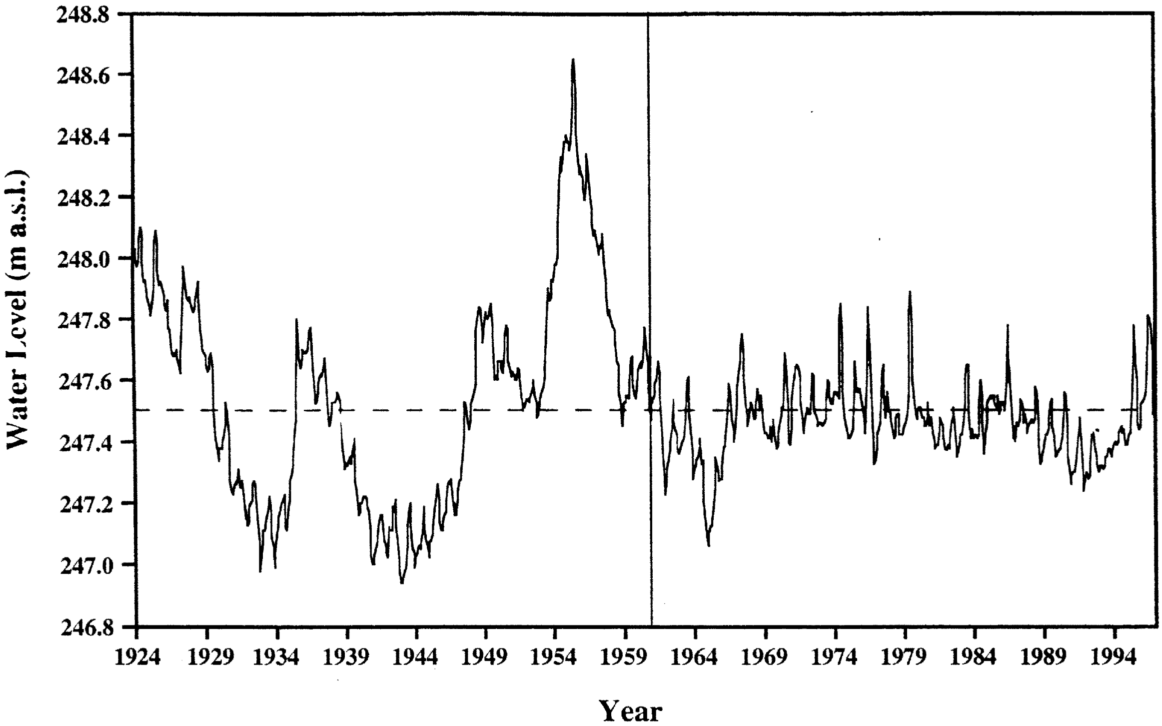

Figure 1. Mean monthly water levels for Lake Manitoba, Canada from 1924-1996. The horizontal dashed line is the long-term mean (248.51 m a.s.l.). The vertical line at 1961 separates the pre-regulation (left) and post-regulation (right) periods.

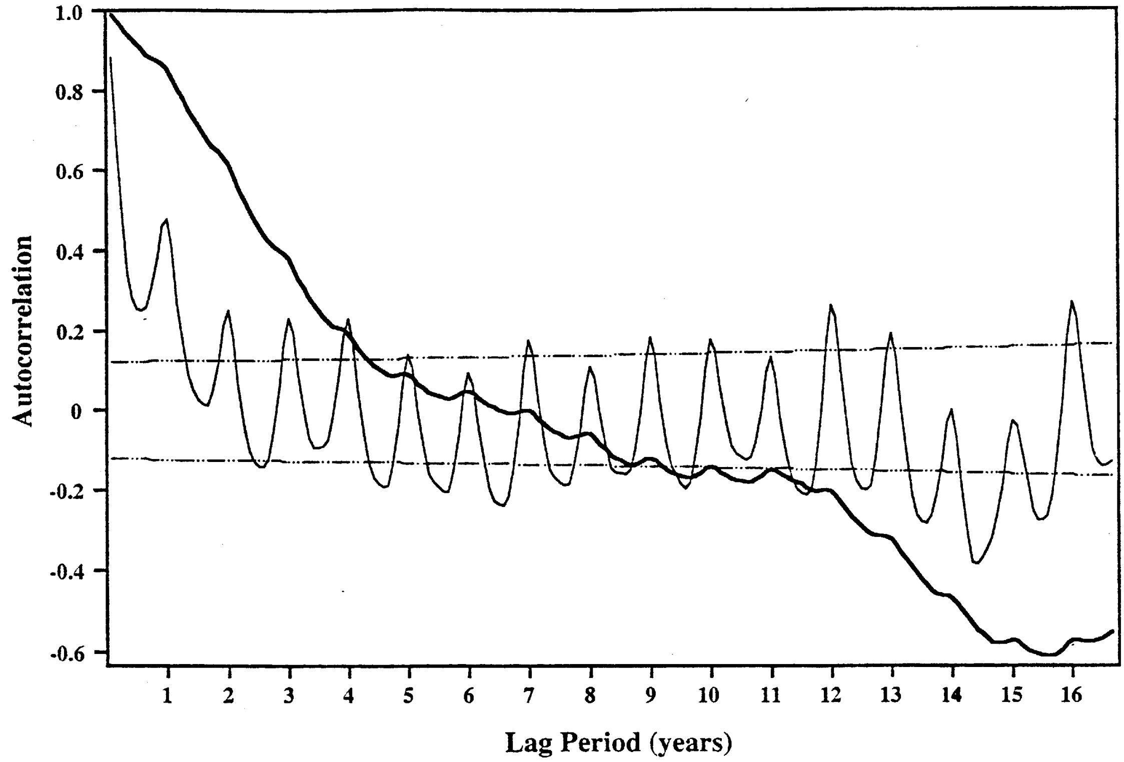

Figure 2. Correlograms for 1924–1960 (thick line) and 1962–1996 (thin line) of mean monthly water levels in Lake Manitoba, Canada. The dashed lines denote the approximate 99% confidence interval.

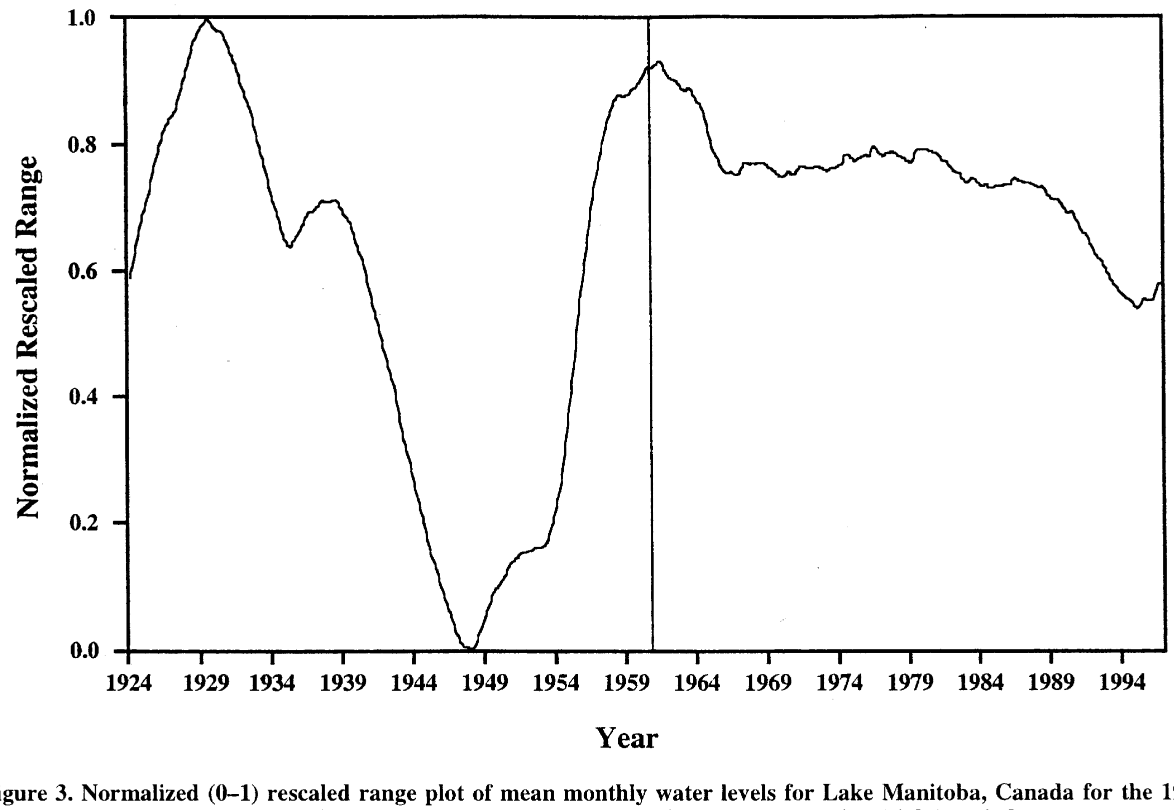

Figure 3. Normalized (0–1) rescaled range plot of mean monthly water levels for Lake Manitoba, Canada for the 1924–1996 period. The vertical line at 1961 separates pre-regulation (left) from post-regulation (right) periods.

trace indicates persistence of values greater than the mean. Prior to 1961, ascending trends were seen for the periods 1924-1929, 1935-1937, and 1949-1960 (particularly the period 1954-1957). By contrast, no strong ascending or descending trends were present after 1961, indicating low persistence. The slight descending trends from 1964-1967, and again from 1989-1993, reflect years of below-normal precipitation.

Discussion

A number of researchers have noted that prolonged 'stabilization' of water levels has highly detrimental effects on shallow northern prairie marshes (Harris & Marshall 1963; van der Valk 1981). Stabilization in this context generally refers to a reduction in the magnitude of water level fluctuations. The magnitude of water fluctuations has certainly declined in the Delta Marsh: prior to 1961, water levels varied by over 1.7 m, whereas fluctuations since 1961 have typically been less than 0.5 m. However, a somewhat different picture emerges if stability is defined in terms of temporal persistence. Fractal time-series analyses revealed that water level fluctuations in Lake Manitoba have become much less persistent since 1961. Since persistence is a relative measure of the 'memory' or temporal predictability of a system (Schroeder 1991), a less persistent system can be viewed as being more 'chaotic' or less 'stable'. One important consequence of lowered persistence is the decoupling of temporal trends in water levels, reducing (or even eliminating) the probability of prolonged flooding or drawdown events in the Delta Marsh.

In practice, both magnitude reduction and lowered persistence of water level fluctuations are probably important in explaining observed changes in the vegetation composition, structure and productivity of Delta Marsh since 1961. Kadlec (1962) found that a single-year summer drawdown had little effect on plant species composition in a flooded boreal wetland. In Saskatchewan prairie potholes, two or more years of continuous flooding, or repeated autumn flooding, were necessary to completely eliminate emergent plant cover (Millar 1973). Along the shores of Lake Erie, it was observed that "generally rising or high water levels" over two or more years (implying high persistence) were required to inhibit the growth of most emergent macrophytes (McDonald 1955). Harris & Marshall (1963) found that drawdown-flooding cycles are important in prairie marsh rejuvenation, but that 3-5 years of continuous flooding may be necessary to eliminate most of the emergent vegetation. They also found that the hybrid cattail can survive in 50 cm of water for up to 5 years.

Similar results have been obtained from more recent experimental studies in the Marsh Ecosystem Research Project (MERP) cells at Delta Marsh. The 10 MERP cells (each 5.5-7.5 ha in size) were flooded to a depth of 248.5 m a.s.l. (ca. 1 m higher than the surrounding marsh) for two years. This prolonged flooding regime almost or completely eliminated five of the seven dominant emergent macrophyte species. For the other species, the cover of hybrid cattail was reduced by ca. 60%, while that of reed grass was reduced by ca. 75% (van der Valk 1994). Following drawdown of the cells, the vegetation that colonized newly exposed substrates differed from that found prior to flooding (van der Valk et al. 1989). Results from controlled experiments in Delta Marsh indicate that depth and duration of floods are both important determinants of spatio-temporal patterns in species distribution and habitat productivity (Neill 1993; van der Valk et al. 1994).

The post-1961 regulation of Lake Manitoba water levels has reduced both the magnitude and persistence of water level fluctuations in the Delta Marsh. This in turn has reduced both the magnitude and duration (persistence) of flood and drawdown events. Shallow northern prairie marshes are disturbance-driven ecosystems that maintain their ecological integrity through periodic, prolonged flood-drawdown events (Harris & Marshall 1963; van der Valk 1981). Such a dynamic environment promotes long-term species coexistence, since the relative competitive abilities of species are in a constant state of flux such that no one species can predominate (Tilman & Pacala 1993). 'Dampening' this natural disturbance regime by water regulation promotes more strongly competitive species at the expense of 'weaker' ones (Grace & Wetzel 1981). Species that presently dominate the Delta Marsh are those best adapted to a temporally 'chaotic' system. Such species are favoured over those requiring the prolonged, higher magnitude cycles that characterized the marsh prior to regulation. Over the past 35 years, cover of the hybrid cattail has increased dramatically, suggesting that this species is very well adapted to a more 'chaotic' (less persistent) environment.

In conclusion, I propose that high environmental persistence is critical to the promotion and maintenance of species-habitat diversity and productivity in northern prairie marshes. Controlled experimental investigations should be undertaken to test this hypothesis.

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