Flow reversals as a driver of ecosystem transition in Florida's springs

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Abstract: The springs of northern Florida have degraded dramatically over recent decades, and filamentous algal mats have replaced submersed macrophytes. The unique temporal stability of these spring ecosystems has prompted narratives about the mechanisms of change in which authors focused entirely on press disturbances, such as NO_3^- enrichment and flow reduction. We tested the hypothesis that pulse disturbances, in the form of episodic flow reversals, are a key component of spring degradation. During flow reversals, acidic floodwaters rich in dissolved organic C (DOC) from adjacent blackwater rivers dramatically alter the light environment, and DOC respiration depletes dissolved O_2 (DO), thereby creating a trophic cascade wherein negative effects on algae consumers enable algal proliferation. Synthesis of river and aquifer stages from springs in the Suwannee River basin indicates that reversal events have become more frequent with time in response to aquifer declines attributed to climate variability and groundwater pumping. This increase in frequency and duration of flow reversal is remarkably concurrent with the emergence of nuisance algal mats. Furthermore, re-analysis of existing algal abundance data suggests that potential for flow reversal is a significant predictor, but only when conditioned on spring DO concentrations. In low-DO springs, algal cover is always high, and reversals have little effect. However, in high-DO springs, algal cover is low except where reversals are likely. Our results suggest that despite remarkable temporal stability, episodic flow reversals may play a key role in regulating the ecosystem state. Focusing on these pulse events may be critical to spring protection and restoration.
Key words: spring, estevelle, reversal, algae, disturbance, pulse

Ecological changes can arise from pulse (i.e., episodic, acute) and press (i.e., persistent, chronic) disturbances. Regime shifts in ecosystems often result from the combination of press disturbances (e.g., P enrichment in shallow lakes, grazing in desert wetlands) that alter ecological resilience and pulse disturbances (e.g., floods, fires) that trigger a switch to an alternative stable state (Suding et al. 2004). Predicting and remediating undesirable ecological changes requires understanding the relative importance of and interplay between the various modes of disturbance, their mechanisms of operation, and their time-scales of action.

The karst springs of north Florida are iconic freshwater ecosystems that support a unique and vibrant aquatic community (Odum 1957a, b) and provide considerable cultural and economic value. The ecological and aesthetic value of springs stems largely from clear, constant discharge (Odum 1957a, b, Duarte et al. 2010), which enables existence of dense beds of submerged aquatic macrophytes (typically *Sagittaria kurziana* and *Vallisneria americana*) that form the base of a charismatic food web of fish, birds, and reptiles. Over the past several decades, many springs have exhibited alarming state transitions from dominance by these macrophytes to dense mats of benthic filamentous algae, principally *Lyngbya wollei* and *Vaucheria* spp. (Stevenson et al. 2004, Quinlan et al. 2008). Remediation of this transition is a central, and broadly publicly supported, regulatory objective for regional water management (FSI 2007).

In part because of the unique temporal stability of these springs (Odum 1957a, Heffernan et al. 2010a), the prevailing narrative for ecological in change in Florida's springs emphasizes the press disturbance of widespread and dramatic NO_3^- enrichment in the Floridan aquifer source. Proponents of this line of reasoning argue that NO_3^- enrichment, in some springs 10 to 100× background concentration (~0.05 mg N/L), has led to lotic eutrophication and algal proliferation. New regulatory standards (0.35 mg N/L) have been adopted to reduce NO_3^- enrichment with the intent of improving ecological conditions. However, the connection between NO_3^- enrichment and enhanced rates

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of ecosystem primary production (Odum 1957a, Canfield and Hoyer 1988, Duarte and Canfield 1990) or algal growth (Cowell and Silver Botts 1994, Notestein et al. 2003) is remarkably weak. Moreover, the ~0 (and nonsignificant) correlation between NO_3^- concentrations and various measures of algal abundance, either within (Cowell and Silver Botts 1994, Hoyer et al. 2004) or across (Heffernan et al. 2010b) springs, suggests that reducing NO_3^- to preclude or reverse ecological change is, by itself, unlikely to be effective.

Alternative narratives for press disturbance also have emerged. Proponents focus primarily on direct and indirect effects of changes in spring discharge. In many springs, discharge has declined relative to historic conditions (Copeland et al. 2009) because of decreased precipitation driven by long-term climate cycles (e.g., warm phase of the Atlantic Multi-decadal Oscillation; Enfield et al. 2001, Kelly and Gore 2008) and increasing groundwater withdrawal (Marella 2014). Increased impervious surfaces associated with urbanization reduce infiltration, though this effect may be small relative to other drivers (Weber and Perry 2006, Khare et al. 2012). Reduced discharge may directly enable algal accumulation by reducing bed scour (King 2014). Declining flows also increase the contribution of deeper, older groundwater (Toth and Katz 2006, Martin et al. 2016) that has markedly lowered spring water dissolved O_2 (DO) over the last 30 y (Heffernan et al. 2010b). DO exerts strong control on the health and composition of the invertebrate community, particularly on densities of gastropods (Dormsjo 2008, Liebowitz et al. 2014) and fish (Odum and Caldwell 1955, McKinsey and Chapman 1998). This indirect effect of flow, which creates a trophic cascade mediated by the deleterious effects of low DO on herbivores, may explain why DO is the best bivariate predictor of algal abundance across springs (Stevenson et al. 2004, Heffernan et al. 2010b).

NO_3^- concentrations and consumptive aquifer pumping have increased more or less steadily for >50 y. However, the transition to algae-dominated systems in many springs has been both recent and rapid. Assessments from the mid-1990s note dominance of vascular plants, diatoms as the primary algal taxa, and scarcely mention filamentous algae (Mattson et al. 1995), but by 2004, filamentous algal mats were widespread (Stevenson et al. 2004). Press disturbances may have pushed the system steadily toward a critical threshold, thereby enabling a rapid transition to a stable algae-dominated state, but pulse disturbances are frequently the proximate causes of system state transitions (Beisner et al. 2003, Suding et al. 2004). One reason for a singular emphasis on press disturbances to explain springs degradation is that short-term pulses in discharge and water chemistry are, at first glance, notably absent.

Many of the large and iconic springs (e.g., Silver, Ichetucknee, Rainbow, Wakulla) discharge to a spring-run that flows for several kilometers before discharging to larger rivers, lakes, or the sea. Because of their length, downstream boundary head conditions exert limited flow control, and the upstream head boundary, controlled by the aquifer, is uniquely temporally stable (coefficient of variation in discharge = CV_Q = 10%; Jawitz and Mitchell 2011) and responds to precipitation forcing with lags measured in months. This remarkable flow stability is paralleled by equally time-invariant water chemistry. In contrast, many springs discharge directly to adjacent large, blackwater rivers. Discharge in these systems is controlled by the head differential between the aquifer and the river to which they flow (Hensley et al. 2015). Because river stage rises far more rapidly and dramatically with rainfall inputs than does aquifer stage, these springs, known as estevelles in the karst lexicon, can reverse flow. That is, under baseflow conditions, when aquifer heads are typically higher than river heads, spring flow is positive (out). This head gradient reverses when the river floods, creating short-duration flow reversals, or negative spring discharge.

These pulse reversals affect a variety of ecosystem attributes. During the early phase of longer reversals (i.e., several days or more) when river stage is rising, acidic river water (pH ≈ 4) highly enriched in dissolved organic C (DOC) floods the spring pool and penetrates into the aquifer (Gulley et al. 2011, Brown et al. 2014). This tannin-rich water (Fig. 1) reduces light penetration and dramatically lowers water-column alkalinity. Strong evidence of light control on macrophyte distribution and abundance (Canfield and Hoyer 1988, Hoyer et al. 2004), light-driven competitive interaction between vascular plants and macroalgae (Szafraniec 2014), and the central role of calcareous-shell-forming gastropods in spring-ecosystem food webs support the potential significance of this first phase of a flow-reversal pulse. On the latter (and longer) phase of a reversal, as positive head gradients between the aquifer and river reestablish when river stage falls, river water entrained in the aquifer during the flood flows back out. During bank storage of flood water, respiration of river DOC can create anoxic conditions and alter availability of solutes associated with low redox potentials, including Fe and Mn (Brown et al. 2014). Prolonged DO declines during flood recession may negatively affect invertebrate grazers, potentially enabling algal release from herbivory control (Liebowitz 2013); likewise, increased availability of dissolved Fe may favor algal growth (Kurz 2013). Effects of these pulse disturbances on system structure are not strictly conjectural. Dramatic loss of aquatic vegetation has been documented at Manatee Springs (one of the largest springs along the Suwannee) immediately following a flow-reversal event (Kurz et al. 2003).

Invoking flow reversals to explain recent changes in spring ecology implies changes in the intensity of these pulse disturbances, and evidence that reversals affect nuisance algal proliferation. To that end, we hypothesized that the frequency and duration of flow reversals in springs ad-

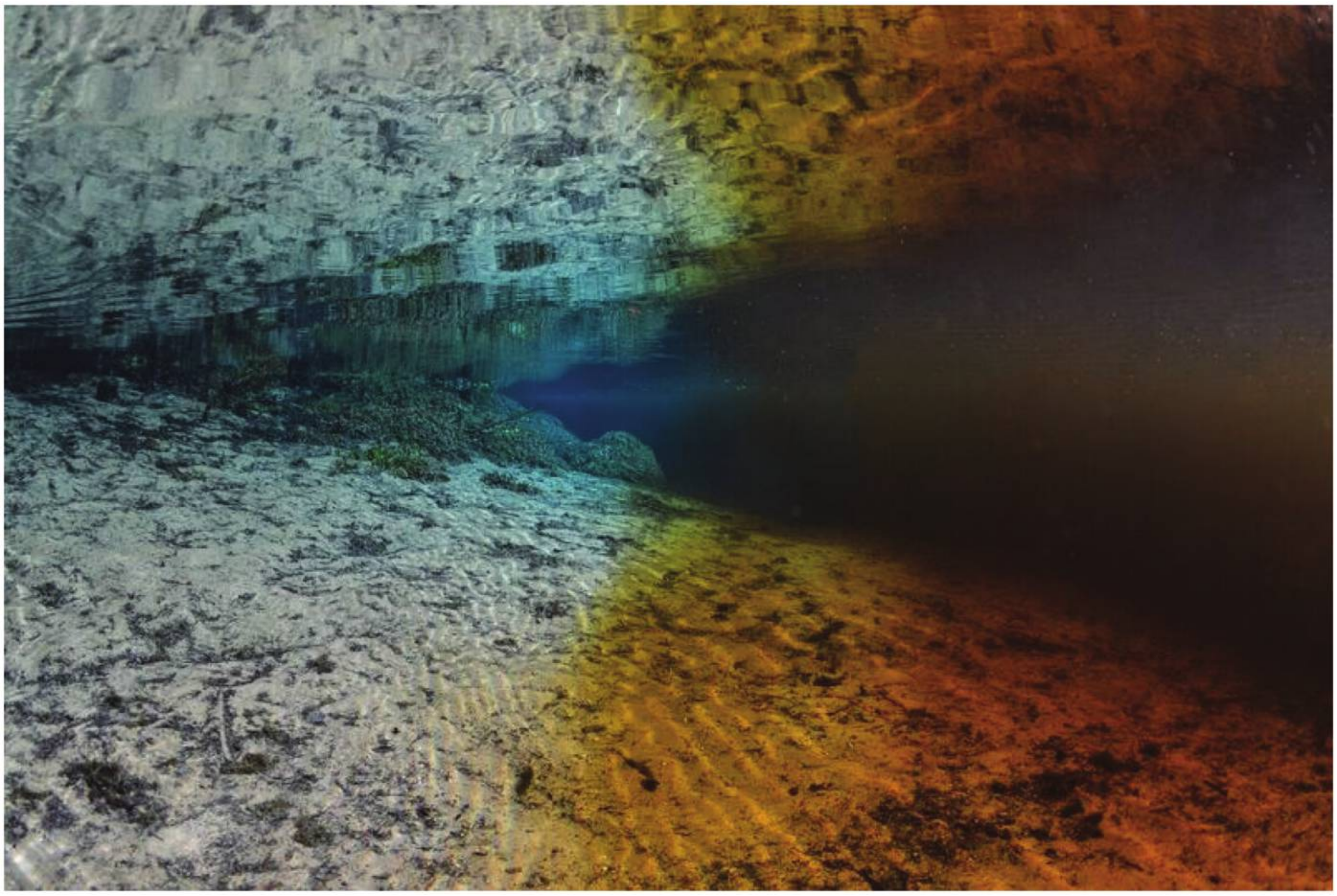


Figure 1. During reversal events, clear, alkaline spring water (left) is displaced by dark, tannin-rich river water (right). Photo courtesy of Jennifer Adler.

jacent to larger rivers has increased over the period during which algal cover has reached nuisance levels (i.e., between 1980 and the present). We further hypothesized that flow reversals are linked to changes in filamentous algal abundance. Confirmatory evidence for both predictions may be of considerable management relevance.

METHODS

To address the changing prevalence and the ecological effects of flow reversals, we synthesized 2 data sets. For the 1st question, we assembled historical data on hydraulic gradients between the aquifer and river. For the 2nd, we reanalyzed algal abundance data from a report spanning 60 springs and numerous measured covariates (Stevenson et al. 2004).

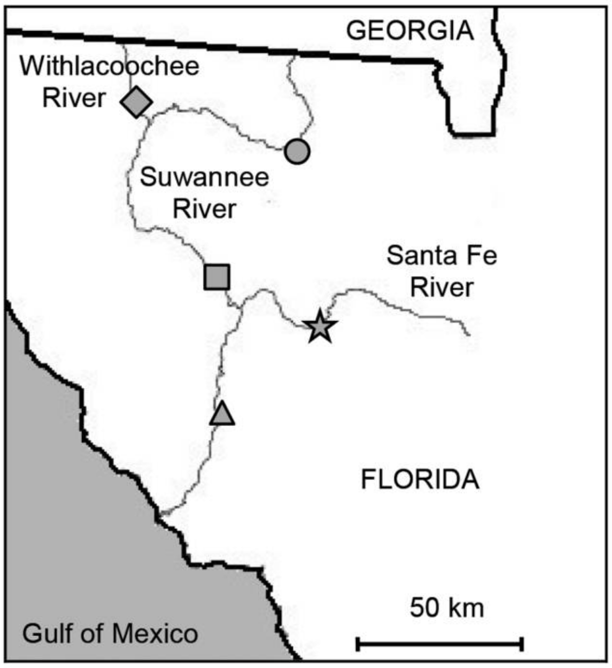
Are the frequency and duration of flow reversals changing?

For our analysis of changing flow-reversal dynamics in springs proximate to flood-prone rivers, we focused on sites within the Suwannee River basin. The Suwannee River drains the coastal plain in southern Georgia and northern Florida, including the Okeefenokee Swamp. The lower Suwannee and its tributaries are home to >½ of the named springs in Florida, and are among those most heavily affected by algal proliferation. Discharge (*Q*) data from the US Geological Survey (USGS) National Water Information System web interface (http://waterdata.usgs.gov/fl/nwis) suggest many of these springs reverse episodically (i.e., the flow record includes negative *Q* values). However continuous *Q* data are available only for selected sites and only for the last decade or so.

To assess whether reversal-event frequency or duration has changed over a longer period, for which continuous *Q* data are unavailable, we developed a method of projecting flow reversals using long-term river and aquifer records, available from the Suwannee River Water Management District water data portal (http://www.mysuwanneeriver.com). We compiled data from the sites with the longest and most complete period of record. We chose 5 sites evenly distributed across the basin: White Springs, Troy Springs, and Fanning Springs along the Suwannee River, Madison Blue Spring along the lower Withlacoochee River (a major tributary of the Suwannee), and Poe Springs along the Santa Fe River (another major tributary) (Fig. 2). We compiled mean daily river stage values. Where river stage data were discontinuous or unavailable at the precise spring-run location, we interpolated data from upstream and downstream gages assuming constant river-water slope. We obtained aquifer stage from wells situated within 10 km of the spring. Measurements typically were monthly, but continuous measurements were available for the most recent years.

This approach yielded historical river and aquifer stage records starting in 1980 and ending in 2015 for all 5 springs. River stage data are available prior to this period, but groundwater data are not. We divided this record into seven 5-y periods and computed the distribution of river stages and aquifer elevations for each period. For each aquifer elevation measurement, we calculated the head difference (ΔH) between aquifer and river. Negative head gradients indicate the potential for spring reversal. We assumed that aquifer measurements were randomly sampled in time to derive the distribution of ΔH values for each 5-y period and calculated the cumulative probability of a negative ΔH. We checked the accuracy of ΔH for projecting flow reversals by comparing values to measured Q for recent years where possible.

At Troy and Poe Springs, the sites where we have nearly continuous daily aquifer elevation measurements over the entire period of record, we calculated the number and duration of distinct projected reversal events. Poe Springs had a few short data gaps, which we filled by linear interpolation). From this analysis, we were able to evaluate whether an increased probability of flow reversal is a result of increased frequency, duration, or both.



Spring	River gage(s)	Aquifer well(s)
○ White	USGS 02315500	SR S021516001
□ Troy	USGS 2320500 USGS 2320000	SR S041329001
△ Fanning	USGS 02323500	SR S091420001 SR S101516017
◇ Blue	USGS 02319300 USGS 2319000	SR S011011002
☆ Poe	SR 02321975 USGS 2322500	SR S081703001

Figure 2. Map showing study sites and list of US Geological Survey (USGS) and Suwannee River Water Management District (SR) gages and wells used in analysis.

Does flow reversal affect spring ecology?

To address the ecological effects of flow reversals, we reanalyzed algal abundance data from a comprehensive survey across 60 springs. (appendix C by Stevenson et al. 2004; http://floridagroundwater.dep.state.fl.us/). Stevenson et al. (2004) measured algal cover and thickness in response to a suite of physical and chemical covariates including depth, velocity, canopy cover, NO_3^-, PO_4^{3-}, Fe, pH, alkalinity, and specific conductance. We divided springs into 3 binary categories. First, we used proximity to a major river as a proxy for likelihood of flow reversal. This metric is imperfect because the occurrence of flow reversals varies with the flood responsiveness of receiving waters, but most rivers in the region change stage dramatically with floods. We considered springs <0.5 km of a major river as likely to reverse, whereas we considered springs that discharge to lakes or have spring runs >0.5 km as unlikely to reverse. We omitted springs that discharge to the sea ($n = 4$) from this analysis. Many such springs exhibit marked ecological decline and may potentially reverse as a result of storm surge, but the prospective ecological effects of these reversals (i.e., increased salinity; Frazer et al. 2006a) are sufficiently different to warrant separate analysis. We defined a 2nd binary category based on dissolved O_2 concentrations (threshold at 2 mg/L). Heffernan et al. (2010b) reported DO as the only significant covariate of algal cover, and Liebowitz et al. (2014) has suggested that low DO can affect grazer populations, thereby enabling algal proliferation. Flow reversals are thought to affect springs ecology primarily by affecting DO, so reversal effects would be most important in springs that ordinarily have high DO, and more muted in springs with persistently low DO. A 3rd binary predictor was NO_3^- concentration, partitioned at the numeric nutrient criteria (0.35 mg N/L).

We used general linear modeling to test the prediction that flow reversals (i.e., adjacent vs distant springs) and DO interact to influence algal cover. We further evaluated interactions with binary NO_3^- class, and main effects of selected continuous water-chemistry variables (specific conductance, PO_4^{3-}, pH). We estimated a global model (all predictors, including 2-way interactions among the binary variables) and selected the best subset of model predictors based on minimizing the Akaike Information Criterion.

RESULTS

Frequency and duration of flow reversals

Time-series of river and aquifer elevations (Fig. 3A, C) exhibit strong event-driven covariance, but with aquifer responses that lag and attenuate the river peak. Most importantly, aquifer levels appear to converge with river levels over time, resulting in lower and more frequently negative values of ΔH (Fig. 3B, D). This occurs most clearly after periods of drought. Monthly values of the modified

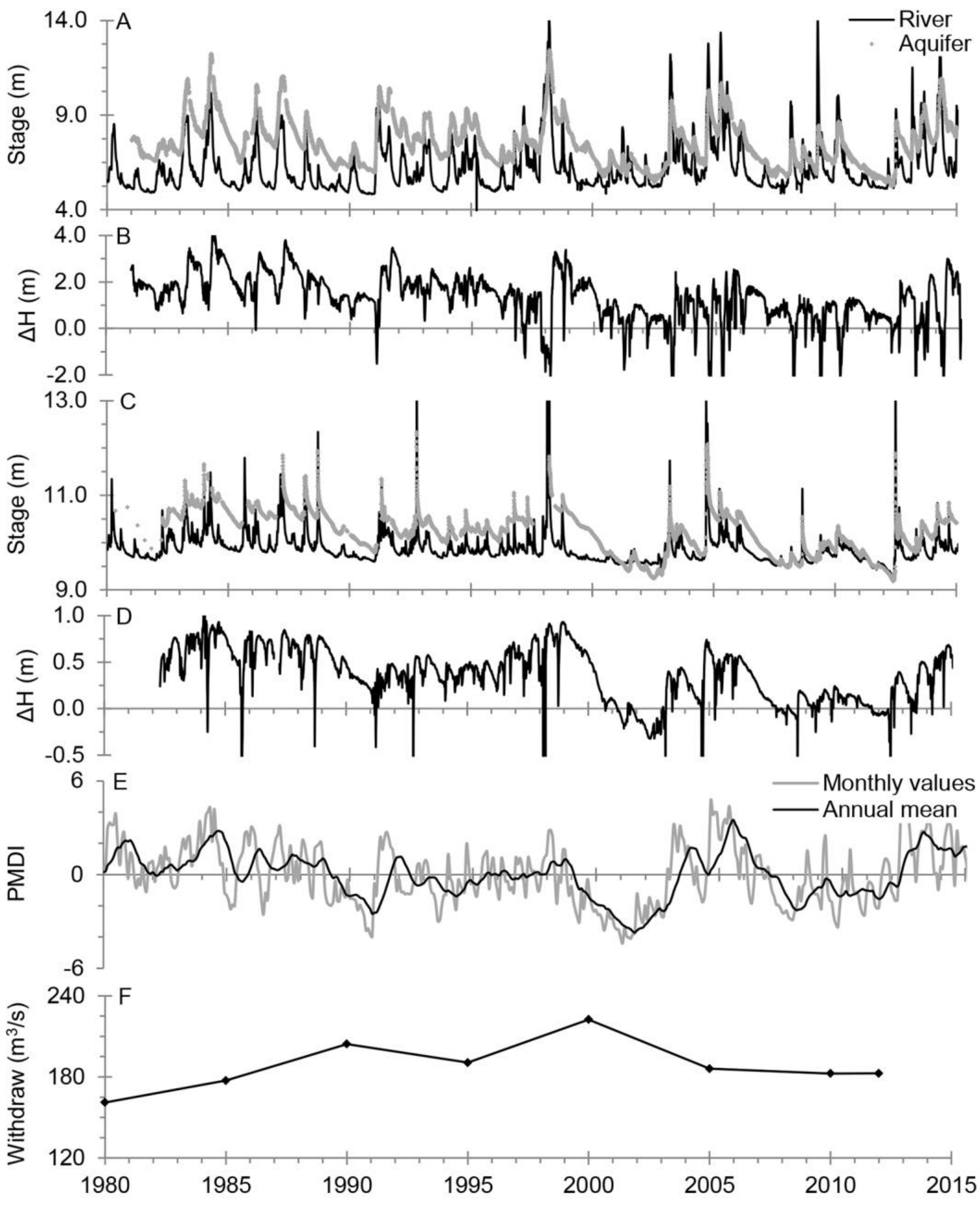


Figure 3. River stage and aquifer elevation (A, C) and head gradient (ΔH) between the river and aquifer (B, D) at Troy Springs (A, B) on the Suwannee River and Poe Springs (C, D) on the Santa Fe River Spring. The progressive convergence between baseflow river stage and aquifer elevation result in more frequent negative ΔH values (B, D) that are largely concurrent with a period of drought (E) and are influenced by increased groundwater withdrawals (F).

Palmer Drought Severity Index (PMDI), and a running average over the preceding year for the Lake City Station situated approximately in the center of the Suwannee River Basin are shown in Fig. 3E (http://www.ncdc.noaa.gov). Aquifer levels also are influenced by increasing groundwater withdrawal rates (Fig. 3F; Marella 2014). Partitioning aquifer declines between climate and consumptive use is a major water-resource challenge that is outside the scope of our paper.

Partitioning river and aquifer levels into 5-y blocks reveals that the distribution of river stages is surprisingly stable with time (Fig. 4A–E). In contrast, aquifer elevation distributions show consistent and dramatic downward trends, strongly confirming the apparent convergence of river stage and aquifer elevation (Fig. 3A–D). In the most extreme case, at White Spring, where discharge has largely ceased, mean aquifer elevation has fallen below mean river stage (Fig. 4A, F). Head differences (ΔH) between the aquifer

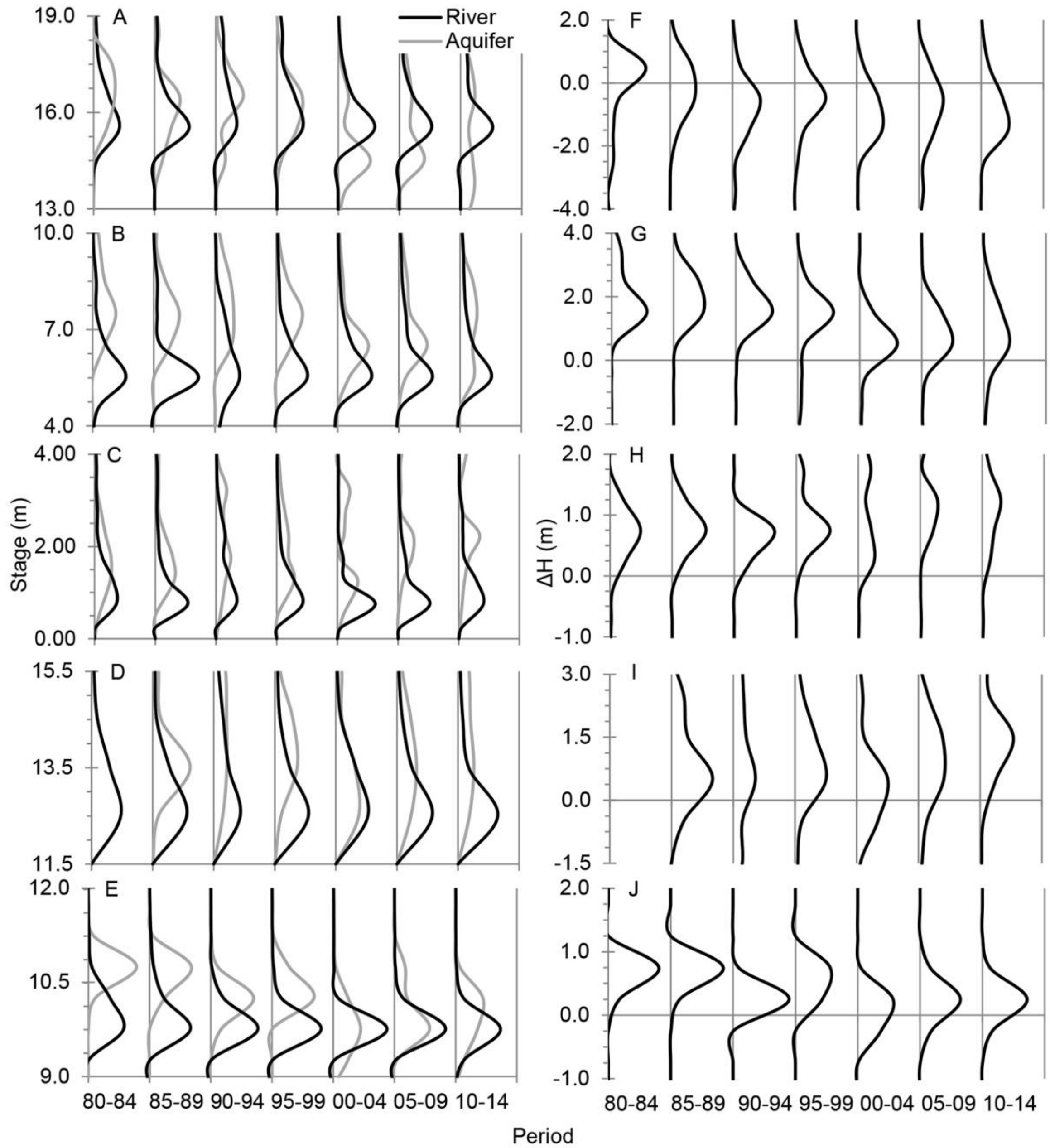


Figure 4. River stage and aquifer elevation (A–E) and head gradient (ΔH) (F–J) between the river and aquifer for White Springs (A, F), Troy Springs (B, G), Fanning Springs (C, H), Madison Blue Spring (D, I) and Poe Springs (E, J) for each 5-y period.

and river have clearly shifted downward with time (Fig. 4F–J), greatly increasing the probability of negative ΔH conditions indicative of flow reversal (Table 1).

Regressing ΔH vs Q tests the utility of negative ΔH as a method of projecting flow reversal. This analysis was limited by the need for Q estimates and aquifer elevation measurements on the same day, both of which are discontinuous over much of the data record. Based on the available data, ΔH and Q were strongly positively correlated ($p < 0.01$) at all sites (Fig. 5A–E). However, some fitted y-intercepts were statistically different from 0, suggesting that use of ΔH may lead to slight overestimation of the frequency of actual flow reversals. This condition potentially arises because of the location of river gages or aquifer wells relative to the spring vent. Provided this offset remains constant, inferences about increasing frequency with time remain robust. Moreover, changing the sign of Q velocity may not be necessary to initiate a press disturbance because even decreased Q caused by declining head gradients can alter both chemical and hydraulic conditions.

At Troy and Poe Springs, continuous aquifer and river elevations allowed us to estimate the frequency and duration of discrete reversal (i.e., negative ΔH) events (Table 2). A clear trend emerges. Relatively infrequent reversals are projected during the early 5-y periods. However, beginning in the late 1990s, a major transition occurs, and the frequency of projected reversal events increases substantially to ~≥10 per 5-y block, and some events last for several months or longer. Many of these longer-term events are evident at the other sites even though we have only monthly data because ΔH values are persistently negative, suggesting regional concordance for the largest events.

Flow reversals and algal abundance

Reanalysis of algal abundance survey measurements yielded 2 models (a global model with all variables and a best-subsets model). Both suggested a strong main effect for DO ($p = 0.006$ and 0.005 for global and subset model, respectively), a weak main effect of flow-reversal ($p = 0.03$ in the global model, nonsignificant in the best-subsets model), and evidence of a highly significant interaction effect ($p = 0.01$ and 0.003, respectively; Table 3). As expected, low DO increases algal abundance, with the fitted main effect indicating that DO < 2 mg/L increases predicted algal abundance by 38%. The weak main effect of flow reversal was opposite to the expected direction, with lower algal abundance in flow-reversing springs, though this effect was not significant in the best subset model. More importantly, the interaction effect between DO and flow-reversal suggests that in low-DO springs, flow reversal has little to no effect, but in high-DO springs, flow reversal has a dramatic effect on algal abundance. In the global model, all other variables (NO_3^-, PO_4^{3-}, specific conductance, pH) were not statistically significant predictors of algal cover (Table 3). However, in the best subsets model, specific conductance (log[SpC]) was significant ($p = 0.05$), with a slope suggesting that springs with higher salinity have higher algal cover independently of DO and reversal effects.

DISCUSSION

Changing patterns of flow reversals

Our results strongly support the hypothesis that flow reversals in the springs along the Suwannee River and its tributaries have increased with time. The dramatic visual convergence of river and aquifer levels over time (Fig. 3A–D) suggests that the magnitude of river flood event necessary to induce a reversal is decreasing. High-stage events capable of initiating flow reversal since the late 1990s would not have produced a reversal in the 1980s. The onset of a new reversal regime is confirmed by a marked increase in the prevalence of negative ΔH (Fig. 4F–J), and further enumerated by the frequency and duration of projected reversal events at Troy and Poe Springs (Table 2). These results suggest that a major and potentially widespread transition in spring hydrology has occurred since the late 1990s, commensurate with observed changes in primary producer community structure (Frazer et al. 2006b, Heffernan et al. 2010b).

The incidence of flow reversals appears to be strongly seasonal. Roughly 80% of reversal events occur between January and April, a period characterized by rainfall from large frontal systems, from which significant runoff occurs because of low evapotranspiration. Moreover, initial aqui-

Table 1. Probability (%) of a negative head differential between aquifer and river at 5 springs in northern Florida.

Site	Period						
	1980–1984	1985–1989	1990–1994	1995–1999	2000–2004	2005–2009	2010–2014
White	34.8	55.4	82.8	72.4	88.1	78.0	83.3
Troy	0.0	0.2	1.5	12.2	16.3	13.2	17.7
Fanning	3.6	0.0	1.8	0.0	5.2	3.5	4.4
Blue	–	18.5	19.2	16.1	32.4	15.0	8.4
Poe	0.6	0.4	1.6	1.6	38.2	18.2	18.4

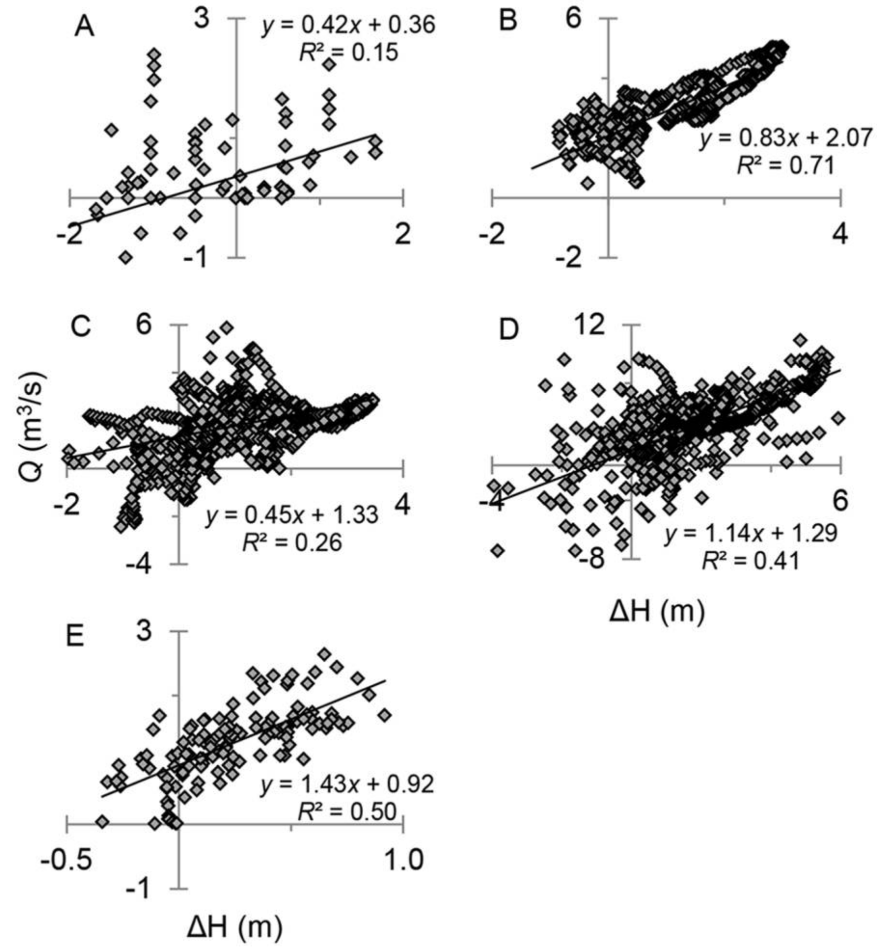


Figure 5. Regressions for discharge (Q) vs head gradient (ΔH) between the river and aquifer for White Springs (A), Troy Springs (B), Fanning Springs (C), Madison Blue Spring (D), and Poe Springs (E).

fer elevations are lower after the autumn–winter dry season. The remaining 20% of events are associated with rainfall delivery from tropical storms. Mean river stage has remained roughly constant over time (Fig. 4A–E), and the frequency of flood events has stayed roughly the same, but the incidence of large floods does appear to increase over the study period. For example, the Suwannee River stage at Troy Springs (Fig. 3A) was >10 m only once from 1980 to 1996, but 9 times from 1997 to 2014. Most of these large events (70%) are springtime floods, not caused by tropical cyclones. The cause for increased incidence of major river floods is unknown, but might be the conjoined effects of changing precipitation patterns and increased watershed impervious surface. However, the effects on spring ecology are potentially significant.

At the 2 study sites for which we have continuous data, we note 2 events of particular significance. First, at Troy Springs a projected flow-reversal event during winter 1997–1998 lasted 153 d. This event is a prominent hydrograph feature at all 5 sites, with gages all along the Suwannee, Withlacoochee, and Santa Fe Rivers exhibiting near record stage. This flood corresponds to the strongest El Niño Southern Oscillation (ENSO) event on record. During ENSO event Florida receives high winter rainfall and streamflow (Schmidt et al. 2001), especially in the Suwannee River (Tootle and Piechota 2004). Second, in 2002, a long-duration projected flow reversal occurred at Poe Springs that was not associated with storm events and high river stage, but with a marked drawdown in aquifer elevations during a period of drought (Fig. 3C). Q records indicate this event may not have been an actual reversal, though markedly low Q did occur. This discrepancy may be the result of gage location and the non-0 intercept of the Q vs ΔH relationship (Fig. 5E). We can document, based both on discharge records and the fact that the swimming area at the county park was closed as a result, that a similar, solely aquifer-driven reversal event occurred in 2011–2012.

The potential role of these single events in resetting ecosystem state is noteworthy. Despite the absence of rigorous monitoring of primary producers, these events are roughly synchronous with the observed degradation of

Table 2. Summary of projected flow-reversal events at Troy Springs and Poe Springs (1980–2015). Q = discharge.

Period	Number of events	Durations (d)	Mean days	Total days
Troy Springs				
1980–1984	0	–	–	–
1985–1989	1	3	3	3
1990–1994	1	26	26	26
1995–1999	5	8, 10, 27, 153, 7	41	205
2000–2004	14	7, 3, 8, 44, 17, 10, 27, 12, 25, 59, 1, 3, 26, 51	21	293
2005–2009	14	42, 2, 14, 11, 5, 41, 10, 13, 9, 12, 7, 36, 21, 30	18	253
2010–2014	16	51, 15, 3, 6, 46, 16, 29, 20, 1, 7, 1, 29, 13, 7, 65, 21	21	330
Poe Springs				
1980–1984	1	6	6	6
1985–1989	2	6, 21	14	27
1990–1994	3	7, 12, 10	10	29
1995–1999	1	40	40	40
2000–2004	8	7, 157, 9, 462[a], 40, 2, 14, 7	87	698
2005–2009	11	5, 15, 51, 2, 5, 86, 128, 13, 15, 5, 7	30	332
2010–2014	8	9, 291[b], 7, 7, 9, 6, 4, 3	42	3367

[a] We could not confirm from discontinuous Q measurements that this event resulted in actual flow reversal.
[b] We can confirm that this event did occur.

aquatic macrophyte communities. The combination of prolonged light attenuation caused by aquifer entrainment of highly tannic flood waters and the potential for persistently low DO conditions as that water is discharged from the aquifer during flood recession suggests these singular long-duration events may have been of sufficient magnitude to induce an ecosystem shift to a regime dominated by high algal densities (Liebowitz 2013). Alternatively, these events may simply mark the transition to more frequent pulse disturbances that maintain favorable condi-

Table 3. Model summary. At top is the global model (all variables, including 2-way interactions among binary predictors). At bottom is the best model based on minimum Akaike Information Criterion. DO = dissolved O_2. Asterisks indicate statistically significant effects and interactions ($p \leq 0.05$).

Model	Notes	Estimate	SE	t	p
Model 1: Global (AIC = 475.7)					
Intercept	$\mu = 7.64$	−196.3	153.4	−1.28	0.21
pH	$\mu = 2.64$	26.1	17.8	1.47	0.15
log(SpC)	$\mu = 0.039$	10.5	6.4	1.65	0.11
PO_4^{3-}	$\mu = 0.039$	−12.4	251.0	−0.05	0.96
DO	2 mg/L = 1	−38.5	13.3	−2.89	0.006*
Reverse	yes = 1	−56.8	25.4	−2.24	0.03*
NO_3^-	>0.35 mg N/L = 1	3.0	19.2	0.15	0.88
DO × Reverse		77.2	29.5	2.62	0.01*
DO × NO_3^-		12.2	22.1	0.56	0.58
Reverse × NO_3^-		50.3	32.3	1.56	0.13
Model 2: Best subset (AIC = 471.2)					
Intercept		−3.25	35.7	−0.091	0.93
log(SpC)	$\mu = 2.64$	11.5	5.7	2.03	0.05*
DO	>2 mg/L = 1	−26.2	8.9	−2.94	0.005*
Reverse	yes = 1	−17.3	10.8	−1.59	0.12
DO × Reverse		46.8	15.1	3.10	0.003*

tions for nuisance algae proliferation (e.g., low grazer densities).

Flow reversals and algal proliferation

Our results also lend indirect support for the hypothesis that flow reversals affect nuisance algal proliferation. The likelihood of reversals (i.e., derived from proximity to large rivers) had little effect on algal abundance, but when conditioned on spring-water DO levels, the potential effect of reversals emerged. This interaction effect implies that O_2 is the master variable controlling ecological health in springs, with 2 modes of negative effect. The 1st mode is chronic low DO stress, which increases algal cover regardless of other factors (e.g., flow reversal) via a suite of mechanisms including inhibition of herbivory and elevated Fe availability. A 2nd mode arises in springs with high DO and conditions suitable for high grazer abundance during typical flow conditions (Liebowitz et al. 2014), but where episodic flow reversals are likely. The attendant transient declines in DO appear to exert important control on ecosystem structure (Fig. 6). In support of this inference, we note that even short-term (i.e., 2-d-duration) experimentally induced hypoxia negatively affected algal grazers and led to high short-term mortality and prolonged (i.e., >3 wk) reductions in grazing rate (Liebowitz 2013). As such, our finding that under high DO conditions, flow reversal nearly doubles algal cover implies that DO inhibition of grazers or mobilization of redox-sensitive solutes (e.g., Fe), not light attenuation, probably is the dominant influence pathway.

We point out that the linkage between reversals and algal proliferation is indirect. Direct observation of a spring transition from a macrophyte- to an algae-dominated state after a reversal would be difficult because most reversing

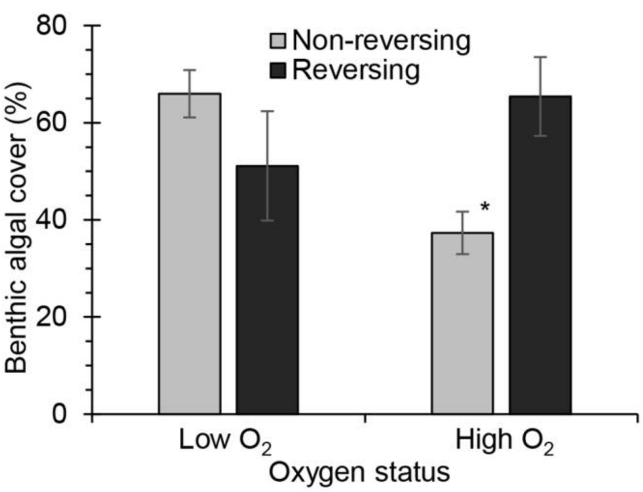


Figure 6. Mean (±SE) algal abundance for springs in 2 binary groupings based on spring vent dissolved O_2 (DO) concentrations (high = >2 mg/L) and reversal likelihood (based on proximity to large rivers).

springs are already algae-dominated. However, previous work has demonstrated the plausibility of a state-transition mechanism at smaller scales (Liebowitz et al. 2014). We also point out that the model does not account for reversal frequency, only whether a spring is capable of reversing, which in turn was based on simple distance from a major river and neglects important site-specific conditions that may preclude reversals. However, the results are consistent with flow reversals influencing ecosystem condition and indicate a critical need to better understand these pulse disturbances and their effects on spring biology.

Flow reversals and the future of Florida's springs

The dramatic changes in flow-reversal frequency and duration since the mid-1990s may be exacerbated by future changes at regional and global scales. In the near term, aquifer elevations may continue to decline with increased groundwater withdrawal. Per-capita consumption appears to be stabilizing because of greater public awareness and management action (Marella 2014), but the growing regional population and increased dependence on southeastern agriculture for national food security suggest persistent, and possibly growing, water demand. Over the next several decades, onset of a cooler phase of the Atlantic multi-decadal oscillation (AMO) (Enfield et al. 2001, Kelly and Gore 2008) is expected to result in increased rainfall and, thus, aquifer recharge, potentially relieving drought stresses accumulated over the last 2 decades. Over longer time scales, global climate change is expected to affect reversal potential in a multitude of ways. Stronger and more frequent ENSO events may increase the magnitude and frequency of both summer–autumn droughts and winter–spring floods. Stronger and more frequent hurricanes also will lead to more high-stage events. Predicted modestly reduced rainfall but elevated temperatures are likely to reduce aquifer recharge and increase irrigation demand which, along with continued population growth and associated water needs, will exacerbate trends in hydraulic head gradients. Last, sea-level rise will affect the downstream boundary elevation of the Suwannee, potentially altering river stage regimes a significant distance upstream. The Suwannee River is a very low-gradient river. Fanning Springs is >50 km from the river mouth, but mean river stage at baseflow is typically only 0.8 to 1.4 m above mean sea level. Thus, forecasted sea-level changes probably will propagate far inland. However, sea-level rise will also increase the elevation of the Floridan aquifer, which is a freshwater lens atop denser salt water.

Uncertainty makes specific projections challenging; our results clearly show that conditions that enhance the frequency and duration of flow reversals are likely to have important ecological effects, and that a new focus on pulse disturbances as a change mechanism relevant to springs function is likely to be integral to their successful protection. For example, the statutory mandate to develop Minimum Flows and Levels (MFLs) for springs, rivers, and aquifers might include the return period and duration of spring reversals as a key consideration. The practicality of designating and achieving a desired reversal regime requires direct attention to management of aquifer elevation given the stochastic nature of flooding. However, attention to basin structural attributes that increase flood size also are relevant. If the algae-dominated state is resilient, management of the pulse disturbance regime alone may be insufficient to ensure reversion to the desired macrophyte-dominated state.

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