

Algal blooms and the nitrogen-enrichment hypothesis in Florida springs: evidence, alternatives, and adaptive management

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Abstract. Contradictions between system-specific evidence and broader paradigms to explain ecosystem behavior present a challenge for natural resource management. In Florida (USA) springs, increasing nitrate (NO_3^-) concentrations have been implicated as the cause of algal overgrowth via alleviation of N-limitation. As such, policy and management efforts have centered heavily on reduction of nitrogen (N) loads. While the N-limitation hypothesis appears well founded on broadly supported aquatic eutrophication models, several observations from Florida springs are inconsistent with this hypothesis in its present simplified form. First, NO_3^- concentration is not correlated with algal abundance across the broad population of springs and is weakly negatively correlated with primary productivity. Second, within individual spring runs, algal mats are largely confined to the headwater reaches within 250 m of spring vents, while elevated NO_3^- concentrations persist for several kilometers or more. Third, historic observations suggest that establishment of macroalgal mats often lags behind observed increases in NO_3^- by more than a decade. Fourth, although microcosm experiments indicate high thresholds for N-limitation of algae, experiments in situ have demonstrated only minimal response to N enrichment. These muted responses may reflect large nutrient fluxes in springs, which were sufficient to satisfy present demand even at historic concentrations. New analyses of existing data indicate that dissolved oxygen (DO) has declined dramatically in many Florida springs over the past 30 years, and that DO and grazer abundance are better predictors of algal abundance in springs than are nutrient concentrations. Although a precautionary N-reduction strategy for Florida springs is warranted given demonstrable effects of nutrient enrichment in a broad suite of aquatic systems worldwide, the DO–grazer hypothesis and other potential mechanisms merit increased scientific scrutiny. This case study illustrates the importance of an adaptive approach that explicitly evaluates paradigms as hypotheses and actively seeks alternative explanations.

Key words: dissolved oxygen; eutrophication; Florida, USA; herbivory; nitrate; precaution; rivers; springs; trophic structure.

INTRODUCTION

How should scientists, managers, and policy makers respond when evidence from their system of interest contradicts expectations based on widely observed, well-understood behavior of comparable systems? While ecosystems do exhibit some genuinely unpredictable behaviors (Paine et al. 1998, Scheffer et al. 2001), most such contradictions result from the application of simplified or inappropriate conceptual models (Doak et al. 2008). Distillation of extant complexity into tractable environmental narratives, often a necessary step for political dialogue, can obscure important underlying uncertainty (Gunderson 2001, Armitage 2004). Given the variation in structure, dynamics, and

conditions among even nominally similar ecosystems, such simplified narratives may be applied to systems where they are insufficient for predicting ecological behavior. Resolving the resulting contradictions between local evidence and the broadly accepted narrative presents a particularly vexing and important challenge. Discounting the importance of a widely observed mechanism may be difficult and, from a precautionary perspective, unwise. At the same time, privileging paradigmatic hypotheses (i.e., shifting the burden of proof from demonstrating the importance of a hypothesized mechanism to demonstrating its inconsequence) may interfere with effective management if consideration of contradictory evidence and alternative mechanisms is limited.

One such well-supported paradigm describes the eutrophication of aquatic ecosystems in response to anthropogenic nutrient loading, which is a widespread threat to freshwater and coastal ecosystems (Dodds 2006, Schindler 2006, Duarte et al. 2009). Although

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correlations between nutrient concentrations and algal abundance (Smith 2006) and increases in primary productivity in response to experimental enrichments (Elser et al. 1990) both support the central hypothesis that nutrient enrichment promotes eutrophication, current models also recognize a more complex set of feedback mechanisms that influence the eutrophication process (Duarte 1995, Carpenter 2003, Duarte et al. 2009). Most notably, a number of studies indicate that food web structure can exert strong control on the response of aquatic systems to nutrient enrichment (Rosemond 1993, Carpenter et al. 2001, Jackson et al. 2001, Hillebrand 2002, Heck and Valentine 2007). Algae in many streams and rivers are limited by nutrient availability (Francoeur 2001, Tank and Dodds 2003, Dodds 2006), but responses of lotic ecosystems to nutrient enrichment remain less well understood than those of lentic and pelagic systems (Borchardt 1996, Hilton et al. 2006, Dodds 2007).

In this paper, we consider the case of benthic algal proliferation in the spring-fed rivers of Florida (USA), arguing that a wide range of observations runs counter to predictions that follow from a simplified eutrophication narrative (i.e., a direct relationship between nutrient enrichment and algal abundance). Consistent with developing conceptualizations of eutrophication in other aquatic systems, we also find tentative evidence that biotic interactions (among algae, invertebrate grazers, and macrophytes) may play a significant role in controlling benthic macroalgal blooms. Nonetheless, we urge a precautionary, adaptive approach to future study and management of springs that includes continued efforts to manage and reduce N loads, along with increased efforts to expand the range of hypotheses under active evaluation. While this study is particular to Florida springs, the explicitly hypothetico-deductive mode of synthesis employed here is likely to be broadly useful as an approach to adaptive management (Holling and Allen 2002). Such an approach requires concerted efforts to describe and evaluate the full range of plausible hypotheses, particularly in cases where scientific paradigms and management tools favor a more singular focus on a particular causal mechanism.

Ecological changes and management response in Florida springs

The karst landscape of north and central Florida contains over 700 named springs (Fig. 1; Scott et al. 2004), a density of large natural artesian springs that is among the highest in the world (Meinzer 1927). Of these, 33 are first-magnitude (historical median discharge $>2.8 \text{ m}^3/\text{s}$ [$100 \text{ ft}^3/\text{s}$]; Fig. 2a), and 191 are second-magnitude ($0.28\text{--}2.8 \text{ m}^3/\text{s}$) springs (Fig. 2b). Below spring vents, resulting runs may flow a few meters or tens of kilometers before entering estuaries or joining rivers fed primarily by surface drainage. Owing to high water clarity and stable hydrology, chemistry, and temperature (Berndt et al. 1998), spring runs

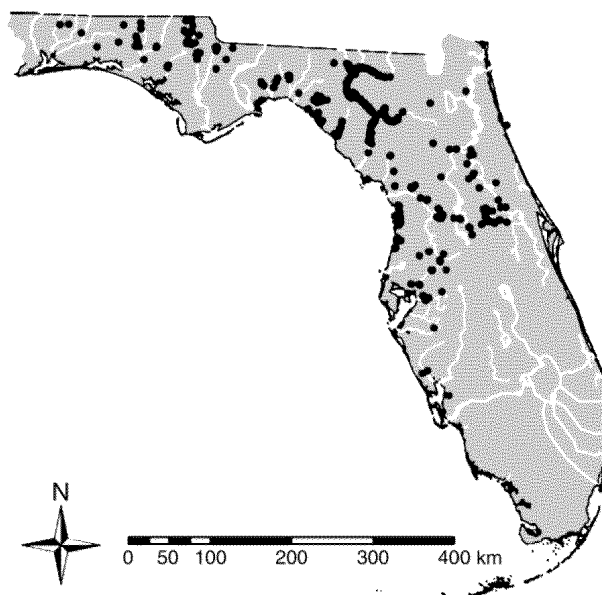


FIG. 1. Distribution of 462 inland springs in Florida, USA, visited by the USGS in 2001 and 2002. Data are from Scott et al. (2004).

historically supported dense beds of submerged vascular macrophytes, typically dominated by *Sagittaria kurziana* and *Vallisneria americana* (Fig. 2c, d). On the basis of their productivity and stability, springs were viewed as natural chemostats and served as models for early studies of ecosystem energetics and trophic structure (Odum 1957a, b).

The springs of Florida have considerable cultural and economic value. During the first half of the 20th century, numerous springs were developed into tourist attractions, and many are now surrounded by state parks or private camping facilities. In 1999, springs within state parks alone received an estimated two million visitors (FSTF [Florida Springs Task Force] 2000). Silver Springs (Marion County, Florida) contributes an estimated \$60 million annually to the local economy (Bonn 2004); estimates of annual economic value for several other major springs range from U.S. \$10 million to \$23 million apiece (Bonn and Bell 2003). Because both the cultural and economic value of springs depend heavily on their natural aesthetic character, real and perceived threats to the biotic structure and function of spring ecosystems are of both ecological and economic concern.

Increasing human use of the north Florida landscape has elevated NO_3^- concentrations in most springs over the past 60 years (Fig. 3). In relatively undisturbed springsheds, and presumably under historic conditions, NO_3^- concentrations in springs range from $0.05\text{--}0.1 \text{ mg N/L}$. The average NO_3^- concentration across the broad population of Florida springs, however, now exceeds 1 mg N/L , and NO_3^- concentrations as high as 7.5 mg N/L have been observed in some springs within the Suwannee River basin (Strong 2004). Mass balance

studies and isotopic composition of NO_3^- indicate that inorganic fertilizers of agricultural and/or residential origin are the primary driver of increasing nutrient concentrations in most springs, but organic point sources such as wastewater treatment facilities and large-scale animal feeding operations may be important in some springs (Jones et al. 1996, Katz 2004, Phelps 2004, Loper et al. 2005). Over this same time period, other macronutrients have not exhibited similar increases in concentration. In fact, ammonium (NH_4^+) and dissolved organic nitrogen concentrations across the broad population of springs have remained relatively low, typically below detection limits; therefore, total nitrogen (TN) flux is dominated by NO_3^- in nearly all Florida springs (Cohen et al. 2007). Soluble reactive phosphorus (SRP), which accounts for almost all total phosphorus (TP), generally ranges from 0.02–0.07 mg P/L and has not increased detectably in most spring systems (Maddox et al. 1992, Scott et al. 2004). Stability of SRP concentrations probably reflects the considerable capacity of the aquifer calcium carbonate matrix to bind orthophosphate (Dillon et al. 2003, Jaber et al. 2006). A few studies have investigated the contamination of springs with synthetic organic compounds such as pesticides and herbicides (Phelps et al. 2006), observing concentrations that, to date, uniformly fall below levels of concern. Reflecting the view of springs as chemostatic systems (Odum 1957b) in which any changes are presumed to be of anthropogenic origin, dynamics of solutes without clear anthropogenic forcing (e.g., dissolved oxygen [DO]) have received little attention.

Beginning in the mid-1980s and into the 1990s, observations of dense benthic macroalgal mats in springs (Fig. 2e, f) became increasingly common. Unfortunately, historic data describing the abundance (or absence) of algal mats, let alone their temporal dynamics, are limited and frequently qualitative. Presently, nuisance algae, particularly *Lyngbya* spp. (a cyanophyte) and *Vaucheria* spp. (a xanthophyte), are found in nearly all springs, covering 50% of spring benthos (Stevenson et al. 2004). Increases in algal abundance are viewed as a decline in the ecological value and integrity of spring ecosystems and have prompted efforts to mitigate ecological change and restore historic conditions (FSTF 2000).

In 1999, the Florida Department of Environmental Protection (FDEP) formed a Springs Task Force charged with determining the causes of declining springs condition and outlining potential policy and management responses (FSTF 2000). In light of the widely demonstrated effects of nutrient enrichment in other aquatic systems, rising NO_3^- concentrations were identified correctly as a potential cause of algal blooms. The Florida Springs Task Force (2000) generally employed cautious language relating NO_3^- enrichment and algal growth; however, despite studies inconsistent with the N-enrichment hypothesis (Odum 1957a, Canfield and Hoyer 1988, Duarte and Canfield 1990,

Cowell and Botts 1994, Terrell and Canfield 1996), the report gave little consideration to alternative hypotheses regarding either ultimate or proximate causes of algal proliferation.

Since the release of the Springs Task Force Report in 2000, the causal relationship between NO_3^- and algal abundance has been increasingly, though often tacitly, accepted by scientists, regulators, and the general public. Recent publications have erroneously cited the Florida Springs Task Force (2000) as concluding that increased NO_3^- concentrations cause algal blooms and other changes in vegetation (Bacchus and Barile 2005, Loper et al. 2005, Toth and Katz 2006). This building consensus is reflected in numerous agency reports and newsletters, newspaper articles, and other media that have publicized the link between NO_3^- and algal abundance. A recent review of the literature relating to the effects of nutrients on Florida springs (Brown et al. 2008) found that studies of landscape-scale N loading to groundwater far outnumbered studies of nutrient effects on spring ecosystems and their constituent biota. While such a distribution of research effort implies that ecological consequences of N enrichment are well understood, Brown et al. (2008) concluded that evidence linking nutrient enrichment to algal proliferation was inconclusive at best.

Considerable political effort and public resources have been expended to reduce N inputs to springs. Such efforts include, for example, a \$160-million bond to finance relocation of a City of Tallahassee wastewater sprayfield connected hydrologically to Wakulla Springs (Loper et al. 2005); the formation of the Suwannee River Partnership, a cooperative effort between state agencies, farmers, and environmental activists (Dederkorkut 2005); requirement of costlier, advanced N-removal septic systems in some springsheds (e.g., Wakulla County Ordinance 2006-58); and the legislation of pollution load reduction goals and total maximum daily loads (TMDL) for the Wekiwa springshed, since set for both N and P (Mattson et al. 2006). Increased NO_3^- in groundwaters and springs are of concern in terms of potential human health effects (at concentrations >10 mg/L [Bruningfann and Kaneene 1993, Ward et al. 2005], which have been observed in some Florida groundwaters [Andrews 1994]), endocrine disruption in springs fauna (Camargo et al. 2005, Guillette and Edwards 2005), and eutrophication of downstream aquatic systems (Smith et al. 2006, SJRWMD [St. Johns River Water Management District] 2007). However, mitigation of algal growth in springs has been the primary rationale for management of N loads (FSTF 2000).

EVALUATING THE NITROGEN-LIMITATION HYPOTHESIS

The specific hypothesis evaluated here is that increasing NO_3^- concentrations in Florida springs have alleviated nutrient limitation, promoting higher growth rates of algae that have led to the proliferation of macroalgal blooms in Florida springs. While this

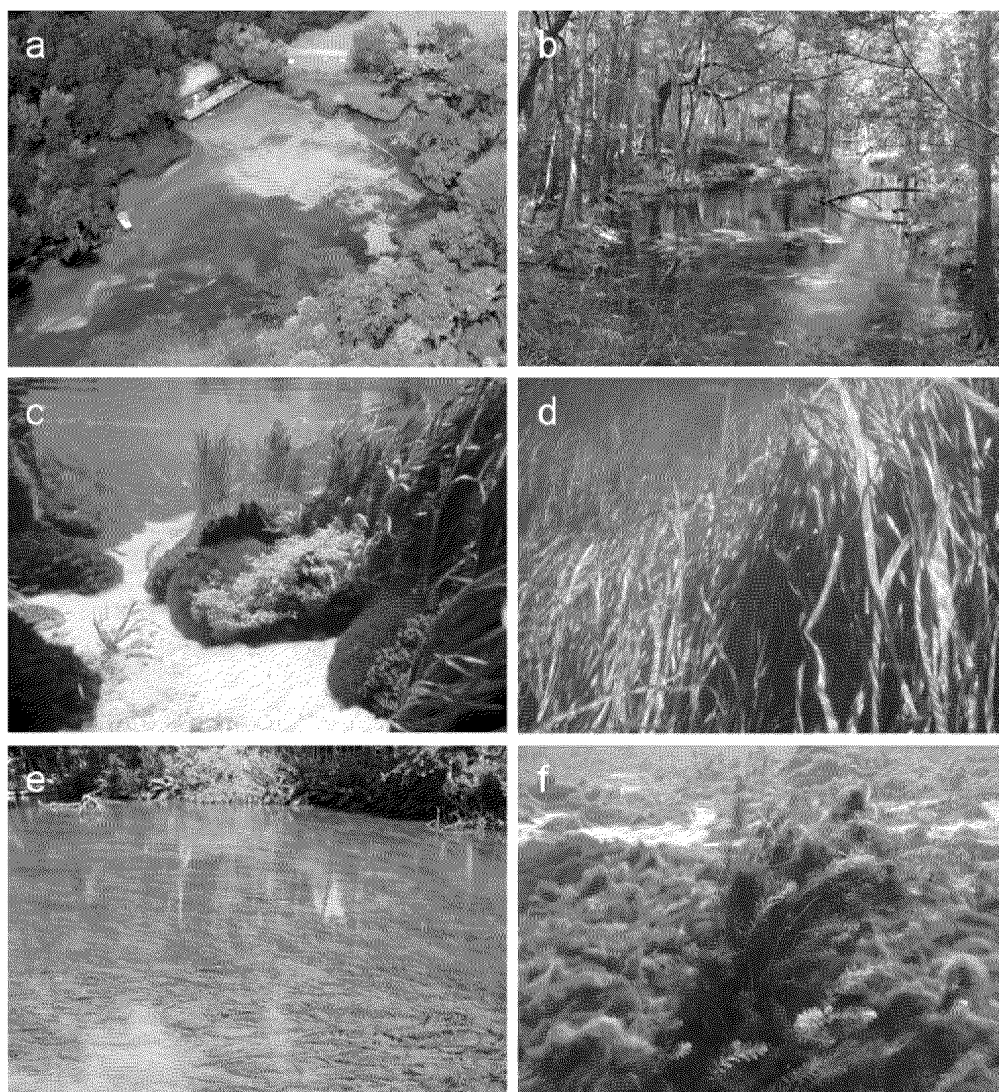


FIG. 2. Vegetation communities of Florida springs: (a) aerial view of Rainbow Springs, a first-magnitude spring group (photo from Scott et al. [2004]); (b) Mill Pond Springs, a second-magnitude spring that discharges to the Ichetucknee River (photo by Larry Korhnak); (c) beds of *Sagittaria kruziana*, largely free of epiphytic growth, in the Ichetucknee River (photo from DuToit [1979]) and (d) Weeki Wachee River (photo by Tom Frazer); and (e) diatoms overgrowing a *Vallisneria* bed in the Chassowitzka River (photo by Tom Frazer). (f) The bed of Crystal River, dominated by filamentous algae on the benthic surface and on nonnative submerged macrophytes (photo by Tom Frazer).

hypothesis is clearly oversimplified given our current understanding of eutrophication (Duarte 1995, Dodds 2006), it is nonetheless the hypothesis most frequently advanced within the context of springs policy and management (FSTF 2000) and most often evaluated by investigators studying the ecology of Florida springs (e.g., Cowell and Botts 1994, Stevenson et al. 2004). Our approach (adaptive inference; Holling and Allen 2002) is to utilize available data and analyses to evaluate a suite of predictions that follow from the N-limitation hypothesis. First, the N-limitation hypothesis predicts positive relationships among NO_3^- concentration, algal abundance, and primary productivity within and among springs through time. Second, the mechanistic basis of the N-limitation hypothesis, namely that nutrient supply

at historic concentrations was insufficient to support algal proliferation, leads to two predictions: at the fine scale, experimental nutrient enrichment should lead to increased algal growth; at the ecosystem scale, ratios of nutrient supply and demand under historic concentrations should correspond to observations from other systems where nutrient limitation has been demonstrated.

Spatial and temporal patterns of nutrients, algae, and productivity

Variation in NO_3^- concentrations among springs provides a natural gradient for evaluating the N-limitation hypothesis. Early studies found no significant relationships between nutrient concentrations and total vegetative biomass in Florida spring-fed systems

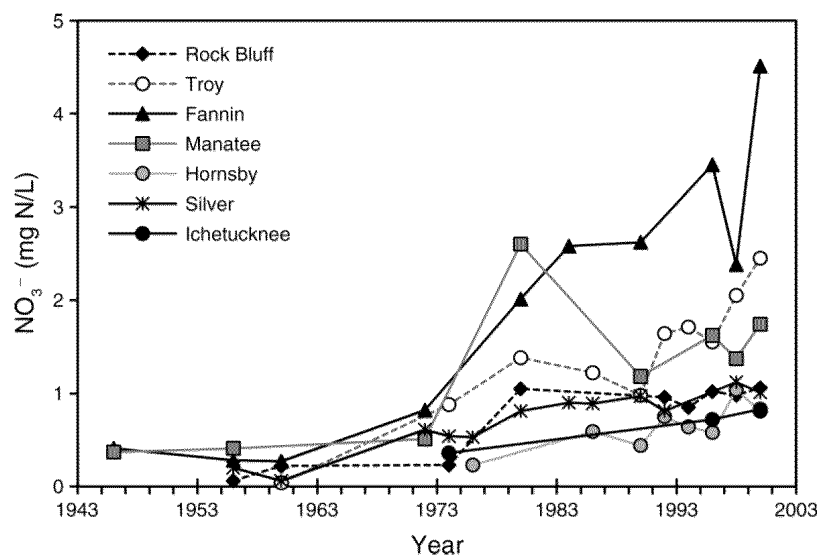


FIG. 3. Changes in NO_3^- concentrations in selected springs. With the exception of Silver Springs, springs shown are within the Suwannee River Water Management District, but NO_3^- has increased in springs throughout Florida. Data are from Hornsby et al. (2004) and Munch et al. (2006).

(Canfield and Hoyer 1988, Duarte and Canfield 1990). More recently, two comprehensive surveys (covering 60 sites in 28 springs) found no statistically significant relationships between macroalgal cover and either total nitrogen (TN [nearly equivalent to NO_3^-]; Fig. 4) or total phosphorus (TP; data not shown) or other metrics of overall algal abundance (Stevenson et al. 2004, 2007), despite the inclusion of springs with concentrations of NO_3^- ranging from historical (<0.1 mg $\text{NO}_3\text{-N/L}$) to significantly enriched (>1 mg $\text{NO}_3\text{-N/L}$). Thus patterns among spring systems provide no support for a link between NO_3^- and algae.

Downstream declines of NO_3^- that occur in many spring runs and rivers (Hoyer et al. 2004, Kurz et al. 2004, Mattson et al. 2006) provide another gradient for evaluating relationships between N and algae. Downstream declines in algal abundance have been observed in the Wekiva River and Rock Springs Run (see Appendix D in Mattson et al. 2006), as well as in three spring-fed coastal rivers (Frazer et al. 2006b). In their extensive survey of springs, Stevenson et al. (2004) found that algal cover and biomass were higher near headsprings than downstream, and that significant algal mats occurred almost exclusively within 250 m of spring vents. While NO_3^- concentrations do decline downstream, elevated concentrations typically extend the entire length of spring runs (i.e., 10 km or more) in NO_3^- -enriched systems (Kurz et al. 2004, Mattson et al. 2006, De Brabandere et al. 2007). This mismatch between the downstream extents of elevated NO_3^- concentrations and algal abundance is inconsistent with the N-enrichment hypothesis.

Several studies suggest that variables besides NO_3^- exert more influence over algal distribution and abundance. In the coastal spring-fed Crystal River, conductivity and alkalinity were the best predictors of *Lyngbya*

abundance, while NO_3^- concentrations provided little predictive power (Cowell and Botts 1994). Hoyer et al. (2004) concluded that flow, light, and salinity were the most important factors determining macrophyte and algal abundance within three nearby coastal rivers, although they did observe a weak positive relationship between NO_3^- and macroalgal biomass. In the springs of the Ichetucknee River, periphyton abundance is highest in springs with low dissolved oxygen (DO) and high soluble reactive phosphorus (SRP), and lower in those with the highest NO_3^- (Kurz et al. 2004).

Although current algal distributions exhibit little relationship to current NO_3^- concentrations, the temporal coincidence between NO_3^- enrichment and the

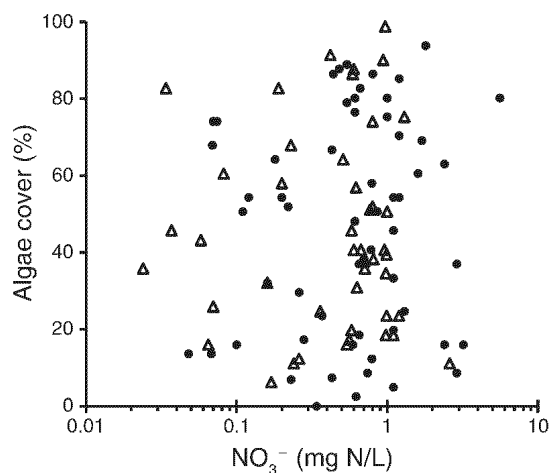


FIG. 4. Nitrate concentration is uncorrelated with algal cover across 60 sites within 28 Florida springs in fall 2002 (closed circles) and spring 2003 (open triangles). Data are from Stevenson et al. (2004) and include a number of springs with NO_3^- concentrations similar to those observed historically (<0.1 mg $\text{NO}_3\text{-N/L}$).

establishment of benthic algal mats during the latter part of the 20th century has been a central line of evidence presented in support of the N-limitation hypothesis (Stevenson et al. 2004, Loper et al. 2005). In most cases, inferences regarding temporal relationships are based on only a few widely separated and qualitative observations, with little description of temporal dynamics at annual or even decadal time scales. For example, photographs of Weeki Wachee springs suggest abundant macrophytes and minimal algae in the 1950s (<0.05 mg $\text{NO}_3\text{-N/L}$), while by 2001 (>1 mg $\text{NO}_3\text{-N/L}$) macroalgae was the dominant benthic cover (Stevenson et al. 2004). In two adjacent spring-fed spring systems, more recent observations indicate that decreased macrophyte and macroalgal cover and increased periphyton on remnant macrophytes coincided with increases in NO_3^- and SRP between 1998–2000 and 2003–2005 (Frazer et al. 2006b).

In some springs, nutrient enrichment appears to have preceded establishment of algal mats by a considerable period. Benthic algal mats were described as a “negligible” component of primary producer biomass in Silver Springs during the 1950s when NO_3^- concentrations were already 0.45 mg N/L (Odum 1957b). Although epiphytic algae were abundant in the 1950s (Whitford 1956), algal mats remained largely absent through the late 1970s as nitrate concentrations rose to ~ 0.7 mg N/L; however, they were widespread by 2005, when concentrations surpassed 1 mg N/L (Munch et al. 2006, Quinlan et al. 2008). In the Ichetucknee River, algal mats were observed in the late 1990s, but vegetation was largely free of epiphytic algae in the late 1970s (DuToit 1979; Fig. 2c) when concentrations already exceeded 0.5 mg N/L (Fig. 3).

Observations of algal responses to nutrient reduction have been limited to date, but the 1992 closing of a wastewater treatment plant in the Kings Bay/Crystal River system provides one case. Declines in TN (from 0.62 to 0.22 mg N/L) and TP (from 0.1 to 0.03 mg P/L) in a small spring run (Cedar Cove) failed to reduce algal abundance even after several years (Terrell and Canfield 1996). Other changes in vegetation structure observed both in Cedar Cove and elsewhere in Kings Bay were attributed to the large 1993 hurricane rather than nutrient reduction (Terrell and Canfield 1996; see also Frazer et al. 2006a). Local stakeholders observed that installation of the wastewater facility predated *Lyngbya* establishment (mid-1980s) by several decades and that *Lyngbya* blooms coincided with storm events and invasive plant management that reduced the abundance of both native and invasive macrophytes (Evans et al. 2007).

The apparent temporal disparity between nutrient enrichment and algal mat establishment has several potential explanations. Delays associated with recruitment and dispersal are unlikely given the presence of *Lyngbya* in springs during the 1950s (Whitford 1956). Given the qualitative and infrequent nature of observations, apparent lags may simply be artifacts of incom-

plete or inaccurate records. Alternatively, internal interactions among algae, vascular plants, and springs fauna may delay the progression of eutrophication (Duarte 1995). In the Kuparuk River, Alaska, for example, bryophyte establishment was observed only after eight years of continuous P enrichment (Slavik et al. 2004), although algal biomass increased significantly in the first year of P addition (Peterson et al. 1993). More generally, rapid increases in growth rate and biomass typify algal responses to nutrient enrichment in lotic ecosystems when nutrient availability is limiting growth (Elwood et al. 1981, Sabater et al. 2005; but see Hilton et al. 2006). A final and equally parsimonious possibility is that other changes (e.g., declines in discharge [Weber and Perry 2006, Williams 2006] or alteration of trophic structure [Munch et al. 2006]) are responsible for the temporal patterns of algal abundance, and that temporal correlations with NO_3^- are spurious.

Little evidence supports the notion that overall primary productivity in springs is limited by nutrient availability. Early comparisons among springs with a wide range of nutrient concentrations found no correlation between N or P concentration and productivity (Odum 1957a, Duarte and Canfield 1990). More recently, a comparison of algal-dominated sites in the Wekiva River and Rock Springs Run to reference sites in Juniper and Alexander Springs found that NO_3^- and gross primary production (GPP) exhibited only a weak negative correlation (WSI [Wetland Solutions, Inc.] 2008). Similarly, in conjunction with the establishment of benthic algal mats, annual GPP declined nearly 33% in the Silver River, from $15.6 \text{ mg O}_2\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in 1979 to $11.2 \text{ mg O}_2\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in 2005 (Munch et al. 2006). These results, while limited to a small number of sites and systems, do not support the positive relationship between productivity and NO_3^- that N-limitation would lead us to expect. Instead, results have been interpreted (Munch et al. 2006, WSI 2008) in terms of a subsidy–stress gradient (Odum et al. 1979), wherein energy or material inputs that initially promote productivity lead to changes in community structure and declines in productivity at higher levels of nutrient loading. However, an equally parsimonious hypothesis is that declines in productivity reflect the changes in vegetation structure, which could occur via a number of mechanisms, rather than an effect of NO_3^- enrichment per se. Moreover, since a positive relationship between nutrient concentration and productivity would certainly be viewed as supporting the N-limitation hypothesis, interpretation of (weak) negative relationships as similarly supportive effectively prevents falsification of the hypothesis on the basis of these data.

Nutrient supply and demand and the hydrologic geometry of springs

Microcosm experiments have generally demonstrated strong nutrient effects on growth rates of algae typically found in springs. Cowell and Dawes (2004) found that

Lyngbya growth rates increased with NO_3^- concentrations up to 0.6 mg N/L in small flasks with slow recirculation (turnover: $\sim 2/\text{d}$), though *Lyngbya* collected from Kings Bay exhibited no response to nutrient additions (Cowell and Botts 1994). Nutrient limitation assays using water from 27 springs indicated P-limitation in 15, N-limitation in six, and co-limitation by N and P in five springs (Stevenson et al. 2004). Stevenson et al. (2007) found growth rate increases at NO_3^- levels up to 0.23 mg N/L for *Lyngbya* and up to 0.64 mg N/L for *Vaucheria* in static microcosms.

Limitation assays conducted in flow-through mesocosms, which more closely simulate hydraulic conditions in springs, have not supported the high limitation thresholds found in microcosms. In one experiment, no effect of NO_3^- on growth rate was observed between 0.1 and 5 mg N/L for either *Lyngbya* or *Vaucheria* (Stevenson et al. 2004). A similar study, conducted with low initial SRP concentrations (0.005–0.009 mg P/L), indicated N-limitation between 0.01 and 0.11 mg N/L for *Lyngbya*, and failed to detect significant variation in *Vaucheria* growth rate (Albertin et al. 2007). Differences between minimum and maximum growth rates were also markedly smaller than those observed in microcosms (Stevenson et al. 2007).

In situ limitation assays also have failed to corroborate enrichment effects documented in microcosms. Notestein et al. (2003) found that P enrichment increased algal biomass accumulation $\sim 30\%$ over 21 days in the N-rich Chassahowitzka River (0.45 mg N/L, 0.015 mg P/L), but N enrichment effects were not significant. Similar experiments in springs with low N concentrations also have failed to detect N enrichment effects; in situ nutrient-diffusing substrates did not induce significant increases in algal abundance, even in low-N springs such as Juniper (0.084 mg N/L) and Gainer (0.16 mg N/L), although loss of replicates lowered experimental power (Stevenson et al. 2004). In low-nutrient Silver Glen and Alexander Springs, *Lyngbya* biomass and productivity exhibited no consistent response to NO_3^- or NH_4^+ addition (PBSJ [Post, Buckley, Schuh, and Jernigan] 2007).

Variation in the magnitude and saturation concentration of growth effects between microcosm experiments and both flow-through mesocosm and in situ experiments can be best explained as an effect of flow. Because flow-through mesocosms more closely simulate extant hydraulic conditions in springs, they likely provide better inference of limiting and saturating concentrations (Borchardt 1996). The similarity of saturating concentrations from mesocosms and historic concentrations provides a potential explanation for muted in situ responses, even in low-N springs: that is, under typical flow conditions in springs, nutrient fluxes are sufficient to satisfy demand even at low concentrations.

Mass balance calculations for N in spring systems similarly suggests that historic fluxes exceed historic (and current) autotrophic demand. Under current

elevated NO_3^- concentrations, plant and algal biomass in spring runs accounts for only a small fraction of N fluxes. Canfield and Hoyer (1988) showed that standing crops over entire spring-fed river reaches (mean length ~ 14 km) accounted for $<0.1\%$ of annual TN flux in eight of 17 systems, and $<1\%$ of TN and TP flux in 15 of 17 systems. The highest standing biomass relative to TN flux (8.5%) was observed in the Wacissa River, where TN (0.2 mg N/L) was near historic levels and areal biomass was five times greater than in any other system. Similar biomass to flux ratios ($<1\%$) were observed in three spring-fed coastal rivers (Hoyer et al. 2004) and two interior spring-fed systems (Sickman et al. 2007). In short, current fluxes greatly exceed demand, even with rapid turnover in macrophytes (3.5/yr; Odum 1957b, Hauxwell et al. 2007) and algae (16/yr; Odum 1957b, Sickman et al. 2007) and without internal recycling.

High nutrient flux vis-à-vis autotrophic demand also confounds the inference that declines in NO_3^- concentrations downstream are due to autotrophic assimilation and indicative of current N limitation in spring ecosystems (Loper et al. 2005, Mattson et al. 2006). In the Ichetucknee River, well-constrained estimates of gross autotrophic N assimilation ($0.12\text{--}0.13 \text{ g N}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$; Heffernan and Cohen, *in press*) are generally $<20\%$ of observed N removal ($0.5\text{--}1.0 \text{ g N}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$; Heffernan et al. 2010). Thus downstream declines in NO_3^- more likely reflect dissimilatory pathways (e.g., denitrification) and provide no support for contemporary N limitation.

Even historic N fluxes in springs would be large relative to demand, particularly in comparison to other lotic systems where nutrient limitation has been demonstrated. Given N assimilation rates reported by Heffernan and Cohen (*in press*), historic N fluxes ($0.05 \text{ mg NO}_3\text{-N/L} \times 9 \text{ m}^3/\text{s} = \sim 39 \text{ kg N/d}$) would be sufficient to support primary production over the entire Ichetucknee River ($8 \text{ km} \times 30 \text{ m} \times 0.13 \text{ g N}\cdot\text{m}^{-2}\cdot\text{d}^{-1} = 31.2 \text{ kg N/d}$), even without N remineralization. For comparison, N flux is equivalent to demand over <100 m of a highly productive N-limited desert stream (Sycamore Creek, Arizona, USA) under late-successional baseflow conditions (Grimm et al. 1981, Grimm and Fisher 1986). Benthic systems in other large rivers exhibit nutrient saturation at low concentrations; in the Athabasca River (Alberta, Canada), for example, P demand is saturated at concentrations as low as 0.003 mg $\text{PO}_4\text{-P/L}$ (Scrimgeour and Chambers 1997). Meanwhile, compared to larger rivers, hydraulic residence times in spring runs is orders of magnitude shorter (seconds–hours vs. days–weeks), limiting the growth potential of pelagic phytoplankton (Hilton et al. 2006). In short, the unusual hydrologic characteristics of large springs provide a potential explanation for observed weak responses to nutrient enrichment.

The N-limitation hypothesis presented in the context of springs management and evaluated here describes a simple relationship between NO_3^- enrichment and algal

abundance. However, responses to nutrient enrichment can be multicausal (Duarte et al. 2009) and are often nonlinear (Duarte 1995, Scheffer et al. 2001, Carpenter 2003). For example, variation among systems can influence nutrient enrichment responses (e.g., basin size and shape in lakes; Scheffer and van Nes 2007). Such complexity could potentially obscure underlying relationships between nutrient enrichment and ecological change. Positive feedbacks between algal mat development and internal nutrient recycling have been suggested as an explanation for the occurrence of algal blooms under low nutrient conditions (Sickman et al. 2007, Stevenson et al. 2007), although this hypothesis fails to explain why benthic algal mats were historically rare in springs or what has caused their recent increase. Interactions among macrophytes, grazers, and algae can produce nonlinear responses to nutrient enrichment (Duarte 1995, Carpenter 2003), but the strength of those interactions and their capacity to produce nonlinear responses to nutrient enrichment remain poorly understood in Florida's springs. Further, macrophytes that compete with and grazers that consume algae are influenced by several other potential disturbances that may contribute to increased algal abundance (Fig. 5).

ALTERNATIVE HYPOTHESES: PROXIMATE MECHANISMS AND ULTIMATE CAUSES

An important early step in understanding the causes of complex ecological phenomena (e.g., emerging infectious disease; Plowright et al. 2008) is to describe the suite of plausible causal pathways that link proximate mechanisms of change in the system of interest to broader environmental dynamics. In lotic environments generally, proximate mechanisms that constrain algal overgrowth (other than nutrient limitation) include physical removal by flow, shading by riparian canopies or aquatic macrophytes, and consumption by grazers. These direct constraints can be linked to broader environmental change via a wide range of intermediaries (Fig. 5). In Florida springs, proximate controls other than nutrient limitation have received relatively little attention, as have the causal pathways that link these mechanisms to broader drivers.

Physical forces acting on long algal filaments are an important constraint on algal biomass accumulation in many lotic environments (Chambers et al. 1991, Hilton et al. 2006). Discharge has declined in many springs over the past 50 years due to both climatic variation and groundwater extraction for municipal and agricultural use (Munch et al. 2006, Weber and Perry 2006, Williams 2006). The effect of flow velocity on the spatial distribution of macrophytes and algal mats in springs (Hoyer et al. 2004, Quinlan et al. 2008) suggests that decreases in discharge might directly lead to increased algal abundance.

Evidence for light limitation in Florida springs (Odum 1957a, Duarte and Canfield 1990) suggests that competitive interactions with vascular macrophytes may

influence the distribution and dynamics of macroalgae. Vascular aquatic plants have been shown to suppress benthic *Lyngbya* mats (Doyle and Smart 1998); conversely, epiphytes and phytoplankton can have detrimental effects on macrophyte growth (Sand-Jensen and Søndergaard 1981, Chen et al. 2007). Negative correlations between submerged macrophyte and macroalgal abundance in springs (Hauxwell et al. 2004, Frazer et al. 2006a, b, Jacoby et al. 2007) are consistent with such competitive interactions. Reductions in macrophyte biomass by recreational use (DuToit 1979, Mumma et al. 1996, PSI [Pandion Systems, Inc.] 2003) or invasive plant management (Cowell and Botts 1994, Evans et al. 2007) may therefore favor establishment of benthic algal mats.

Grazers can reduce algal biomass in freshwater ecosystems and alter responses to nutrient enrichment (Rosemond et al. 1993, Feminella and Hawkins 1995, Carpenter et al. 2001, Hillebrand 2002, Heck and Valentine 2007). In fact, changes in trophic structure alone can permit increases in algal abundance even under low nutrient conditions (Jackson et al. 2001). While studies of herbivory in springs are limited, available data suggest that invertebrate grazers can influence the abundance and productivity of algae (Knight 1980, Dormsjo 2007). The reduced productivity of some algal-dominated springs (Munch et al. 2006, WSI 2008) is consistent with studies in other ecosystems where reduced grazing leads to greater primary producer biomass but decreased productivity (Dyer et al. 1993, Kupferberg 1997, Steiner 2003, Stewart et al. 2006).

Anthropogenic changes in the hydrologic, ecological, and chemical structure of springs could influence the abundance and efficiency of grazers and, potentially, their capacity to suppress algal overgrowth. Low flows and water control structures may exclude large mobile herbivores from springs, as in Silver Springs where fish biomass declined by >60% following the damming of the Ocklawaha River downstream of its confluence with the Silver River (Munch et al. 2006). Decreases in spring flows also could inhibit grazing rates of some invertebrates (Poff et al. 2003). In addition, both invasive plant management and recreational use of springs can dramatically reduce standing crops of vegetation, potentially altering the quantity and quality of habitat available to grazers. Invasive plant management also frequently involves application of herbicides (e.g., diquat dibromides) with known detrimental effects on invertebrate grazers (Evans 2008). Herbicides, insecticides, and other agricultural chemicals have been detected in some springs, although not at levels thought to pose risks (Phelps et al. 2006). The lack of correlation between NO_3^- concentrations and algal abundance suggests that ecotoxicological effects of NO_3^- (Guillette and Edwards 2005) are not a significant cause of reduced grazing, although such effects should still be of concern in their own right.

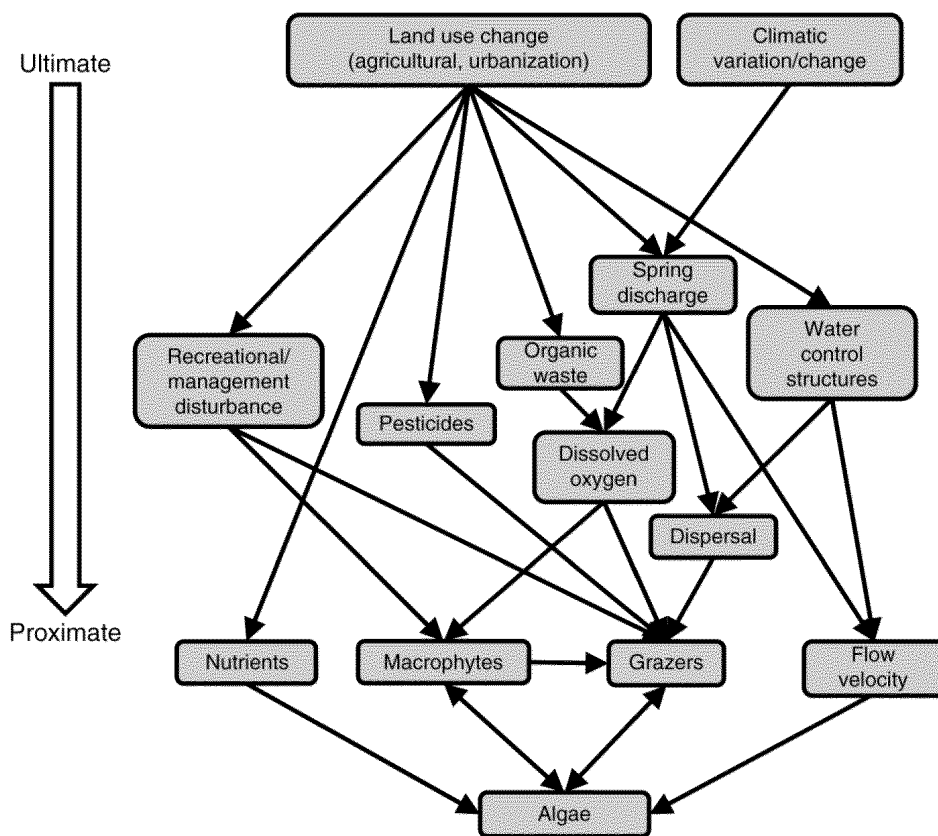


FIG. 5. Hypothesized relationships among ultimate causes, intermediate effects, and proximate mechanisms potentially influencing algal growth in Florida springs. Effective adaptive management of springs would incorporate evaluation of this wider suite of potential influences on algal abundance.

The effects of low dissolved oxygen (DO) on springs biota have received some attention both historically and recently. Hypoxic conditions downstream of low-DO springs reduce invertebrate density and insect emergence (Sloan 1956, Munch et al. 2006, Dormsjo 2007), lower the viability of fish (Odum and Caldwell 1955), and alter community structure (McKinsey and Chapman 1998). Hypoxic conditions may inhibit macrophyte growth (Duarte and Canfield 1990), while many cyanophytes tolerate anoxic conditions (e.g., Gamenick et al. 1997). As a result, low DO could release algae from both grazing pressure and competition with macrophytes for light.

Dissolved oxygen: temporal dynamics and relationships with algal abundance

The current understanding of interactions among spring discharge, DO, grazers, macrophytes, and algae suggests a number of plausible causes of increased algal abundance (Fig. 5), but the temporal dynamics of DO in spring vents and the relationship between DO and algal abundance remain largely unknown. To assess the plausibility of these interactions as causes of algal proliferation, we performed two new analyses of existing data. First, to evaluate whether DO concentrations in springs had changed in conjunction with increased algal

abundance, we used data from Scott et al. (2004) to compare DO concentrations from 1972 with those measured in 2002. Second, we used general regression models to predict algal cover as a function of a suite of variables, using data from Stevenson et al. (2004) that had previously been analyzed with univariate correlations and principal components analysis.

While Scott et al. (2004) report DO from >200 springs during their 2002 survey, data from 1972 were available for only 47 springs. We excluded five sites from this analysis because the location of sampling was unclear for one or both surveys. Within this population of springs, DO declined by an average of 1 mg/L between 1972 (3.03 ± 0.24 [mean $\pm$ SE]) and 2002 (2.00 ± 0.29 ; paired t test: $df = 41$, $t = 4.7$, $P < 0.005$). In addition, the proportion of springs with DO concentrations <1 mg/L (Fig. 6) increased from <5% to >40% (Fig. 6). Whether changes in springs DO between 1972 and 2002 are directional or cyclical is not known, but increased hardness and alkalinity over the same interval (Strong 2004) indicate that decreases in DO may reflect a greater contribution of older groundwater, richer in calcite and lower in DO (Toth and Katz 2006). If so, reductions in flow due to both climate and anthropogenic water use may adversely impact oxygen concentrations at spring vents. Increased loading of human and

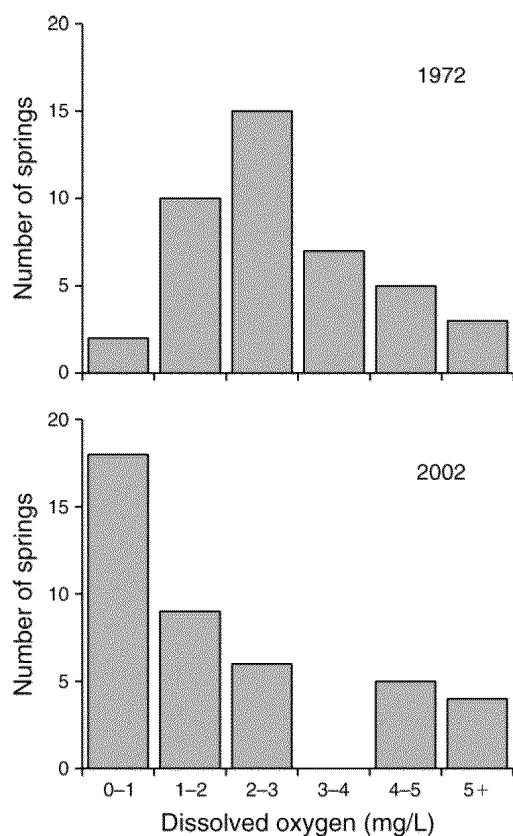


FIG. 6. Dissolved oxygen (DO) concentrations in 42 Florida springs in 1972 and 2002. DO declined by ~ 1 mg/L from 3.03 ± 0.29 (mean $\pm$ SE) to 2.00 ± 0.24 , and the number of springs with DO < 1 mg/L increased from 2 to 18 (out of 42). Temporal dynamics of DO in Florida springs have not previously been evaluated, despite available data. Data presented here are from Scott et al. (2004) and represent all springs for which 1972 data are available. Springs for which only 2002 data were available were not included in our analysis.

animal wastes and associated biological oxygen demand (BOD) could also contribute to this pattern.

Using a general regression model with backwards stepwise procedures ($P = 0.05$ to enter, $P = 0.10$ to remove), we modeled percentage macroalgal cover as a function of DO, temperature, pH, conductivity, total nitrogen (TN), total phosphorus (TP), and the percentage of sampling points qualitatively assessed as having high grazer abundance (Stevenson et al. 2004). We applied this analysis to the subset of sites located within 100 m of spring boils for which all of these predictors were reported (23 and 38 sites in spring and fall 2003, respectively), assessing these relationships separately for each season. In the spring, algal cover was related to DO (negative) and temperature (positive; total model $P = 0.02$, adjusted $R^2 = 0.26$). Although univariate tests did not include grazers as statistically significant, a spring season model (Fig. 7a) with DO, temperature, and forced inclusion of grazers yielded an improved fit over the stepwise approach (total model $P = 0.01$, adjusted $R^2 = 0.35$). In the fall (Fig. 7b), algal cover was significantly

negatively related to DO and grazer abundance (total model $P = 0.02$, adjusted $R^2 = 0.17$; for detailed results of all analyses, see Appendix). The visible outlier in the fall regression plot is Cypress Springs, a site with negligible algal cover and enormous grazer biomass; recent observations (D. Liebowitz, *unpublished data*) at the site confirmed the feasibility of the data, despite its apparent extreme values. We also performed the same analysis including data from sites located farther from spring boils, with spring and fall data treated as independent. In this larger data set ($n = 96$), DO (negative), grazers (negative), and temperature (positive) were significantly related to algal cover, while other variables were excluded (whole-model $P = 0.0005$, adjusted $R^2 = 0.15$). While much of the variance in algal cover remains unexplained, other potentially relevant predictors (e.g., recreational use) were not measured. Given the stability and small range of variation in temperature among springs, the causal mechanism linking temperature and algal abundance remains unclear. Nonetheless, DO and grazer abundance were consistently related to algal abundance, while nutrient chemistry (TN, TP) failed to improve model fit.

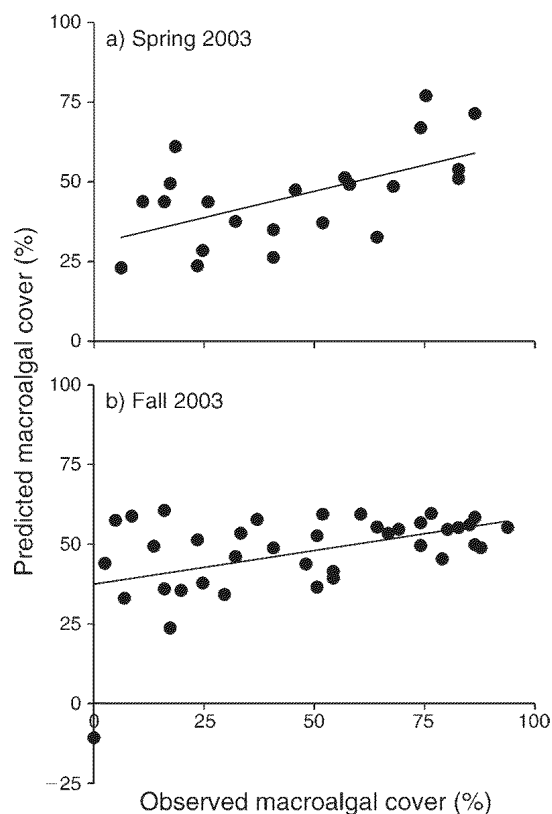


FIG. 7. Predicted and observed values of percentage algal cover in Florida springs in (a) spring and (b) fall 2003. Predicted values are based on relationships with spring vent dissolved oxygen (DO) and grazer abundance in the fall, and vent DO and temperature in the spring. Lines are best-fit regressions based on statistical results reported in the Appendix. Data are from Stevenson et al. (2004).

Other observations provide additional support for the links among DO, grazer density, and algal blooms. In the Ichetucknee River, algal blooms predominantly occur at or just below vents of low-DO springs, which also have lower NO_3^- than the comparatively well-oxygenated springs in that system (Kurz et al. 2004, Frydenbourg 2006). More broadly, the confinement of dense algal blooms to several hundred meters below spring vents (Stevenson et al. 2004) corresponds roughly to the downstream extent of hypoxia in anaerobic springs (Sloan 1956, Odum 1957b). While available data are far from conclusive, the empirical case for the DO-grazer hypothesis is somewhat stronger than the case for the NO_3^- -enrichment hypothesis, despite the relative inattention paid to the former. These observations should motivate more detailed and rigorous field surveys of invertebrate grazer and algal abundance, along with experimental evaluation of the densities at which these consumers are able to control algal biomass.

ADAPTIVE PRECAUTION AND FUTURE MANAGEMENT OF SPRINGS

Adaptive management seeks to reduce tensions between scientific and policy-based perspectives on uncertainty by using responses to management actions to evaluate and refine hypotheses about system behavior (Walters and Hilborn 1978, Walters and Holling 1990). In the case of Florida springs, such tension is exacerbated by contradictions between the body of evidence in spring systems, which is largely inconsistent with the N-enrichment hypothesis, and strong support for the general importance of nutrient enrichment as a cause of eutrophication in aquatic ecosystems. In light of the vulnerability of the upper Floridan aquifer to N enrichment (Cohen et al. 2007), continued implementation of nutrient reduction programs for Florida springs is the appropriate precautionary approach. Resulting declines in NO_3^- concentrations will both allow further evaluation of more sophisticated versions of the N-limitation hypothesis and guard against the risk that nutrient enrichment contributes to algal blooms and other ecological changes in Florida springs. The N-sensitivity of downstream ecosystems (FDEP [Florida Department of Environmental Protection] 1998, SJRWMD 2007) and the ecotoxicological (Guillette and Edwards 2005) and human health effects of NO_3^- enrichment (Bruningfann and Kaneene 1993, Ward et al. 2005) provide strong, additional rationales for such a course of action. However, changes in the chemistry of springs in response to reduced N loading may take decades. More importantly, even the most favorable interpretation of available evidence indicates that N reduction alone may be insufficient to reduce algal abundance. Effective protection of springs will, therefore, require an approach that experimentally addresses a much wider range of proximate and ultimate mechanisms (Fig. 5) that determine the biotic structure of spring ecosystems.

Beyond its implications for the future management of Florida springs, our synthesis illustrates the importance of an adaptive management approach that simultaneously considers multiple hypotheses and incorporates multiple lines of evidence, particularly in the evaluation of favored hypotheses (Plowright et al. 2008). Widely held and well-supported paradigms, such as the link between nutrient enrichment and algal blooms, are easily translated into narratives that engender both oversimplification and overconfidence. Failure to recognize narratives as such reduces the likelihood that alternative hypotheses will be considered and that evidence will be scrutinized carefully (McLain and Lee 1996, Gunderson 2001, Armitage 2004). In Florida springs, emphasis on the N-limitation hypothesis in research, management, and policy has limited efforts to evaluate the importance of other mechanisms. As a result, available evidence linking dissolved oxygen, grazers, and algal abundance largely went unexamined, illustrating that development and evaluation of alternative hypotheses is most critical when broader paradigms and management tools favor the adoption of a single hypothesized mechanism. Explicitly hypothetico-deductive synthesis should play an important role in such efforts.

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APPENDIX

Detailed results of multiple regression analysis predicting algal cover (*Ecological Archives* A020-026-A1).