An aggregation of turtles in a Florida spring yields insights into effects of grazing on vegetation

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Abstract: An aggregation of Suwannee Cooters (*Pseudemys concinna suwanniensis*) prompted an investigation of their effects on vegetation in Blue Spring, a 2nd-magnitude spring in Gilchrist County, Florida. We counted turtles and documented % cover and wet biomass of vegetation in September and October 2013. The maximum mean density of turtles (1566 ± 319 turtles/ha) was recorded near the spring vent during the 1st survey. Mean density among all reaches of the spring run decreased from 421 ± 133 to 145 ± 58 turtles/ha during the 30-d period between surveys. Percent cover and wet biomass of *Hydrilla verticillata*, *Sagittaria kurziana*, and *Vallisneria americana* decreased significantly between surveys, which indicated that turtles reduced the quantity of vegetation in the spring. Relatively little vegetation was lost downstream as turtles grazed, so removal rates were converted to grazing rates. Mean grazing rates on *H. verticillata*, *S. kurziana*, and *V. americana* were estimated to be 850, 275, and 78 g wet mass (WM) turtle^{-1} d^{-1}, respectively. These grazing rates translated to 68, 25, and 5 g dry mass (DM) turtle^{-1} d^{-1} for *H. verticillata*, *S. kurziana*, and *V. americana*, respectively. Per kg of turtle, grazing rates were 17, 6, and 1 g DM kg^{-1} d^{-1}, respectively. These results are the first estimates of *P. c. suwanniensis* grazing rates derived from field data and the first evidence that *P. c. suwanniensis* grazed more heavily on the invasive *H. verticillata* than on native vegetation. These findings highlight the role that turtles play in freshwater food webs, and they underscore the importance of submersed vascular plants as a food source for Suwannee cooters. Managers should consider the implication of reduced food for Suwannee cooters and other herbivorous turtles in Florida's springs as rooted macrophytes are replaced by potentially less palatable, filamentous macroalgae, such as *Lyngbya* sp.

Key words: conservation, freshwater turtles, submersed aquatic vegetation, hydrilla, invasive vegetation

The Suwannee cooter (*Pseudemys concinna suwanniensis*), native to watersheds connected to the northeastern Gulf of Mexico between the Ochlocknee River in Florida's panhandle and the Alafia River near Tampa, occupies rivers, streams, and spring runs where it can find aquatic vegetation for feeding and sites above water for basking (Jackson and Walker 1997, Jackson 2006, Ward and Jackson 2008, Heinrich et al. 2015, Johnston et al. 2016). Historically, the diet of *P. c. suwanniensis* comprised a variety of native aquatic plants and algae, including *Ceratophyllum demersum*, *Cladophora* sp., *Lemna* sp., *Najas* spp., *Podostemon ceratophyllum*, *Sagittaria kurziana*, *Spirogyra* sp., and *Vallisneria americana* (Marchand 1942, Fahey 1987, Lagueux et al. 1995). In recent decades, several investigators observed *P. c. suwanniensis* consuming the introduced exotics *Egeria densa* (Brazilian elodea) and *Hydrilla verticillata* (Bjorndal and Bolten 1992, Lagueux et al. 1995, Fields et al. 2003, Piña 2012). Interactions with *H. verticillata*, which was introduced to Florida ca. 1960 (Florida Springs Task Force 2000), is of interest to managers of natural resources because it often outcompetes native vegetation by reproducing and spreading rapidly and overgrowing and shading other plants (Haller and Sutton 1975, Van et al. 1999). Grazing on *H. verticillata* or other submersed aquatic vegetation by *P. c. suwanniensis* has not been quantified, but the rates could be substantial given that individual *P. c. suwanniensis* can achieve a mass ≥10 kg and populations can approach 600 kg/km in some rivers (Jackson 2006).

A unique opportunity to quantify interactions with submersed aquatic vegetation was created by a large aggrega-

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tion of *P. c. suwanniensis* in Blue Spring, Gilchrist County, Florida (USA), in late summer 2013 (Fig. 1). During the aggregation, turtles were by far the dominant grazers in the spring run, and observations and videos indicated that very little vegetation was lost downstream as turtles grazed. Thus, field surveys of turtles and vegetation yielded estimates of grazing rates that augmented existing knowledge of turtle biology and existing data on trophic webs in Florida spring runs, with the latter insights generating potentially important implications for managers of these aquatic systems.

METHODS

Study site

Blue Spring, a 2^{nd}-magnitude spring in Gilchrist County, Florida (lat 29.82990°N, long –82.68291°W), discharges $>180 \times 10^6$ L of fresh water/day from the Floridan Aquifer (Scott et al. 2004). Three smaller springs deliver additional groundwater to the main spring run, which flows ~0.4 km before its confluence with the Santa Fe River.

We classified the main spring run into 4 reaches for surveys of turtles and 3 reaches for surveys of submersed aquatic vegetation. We analyzed counts of turtles in the spring reach (closest to the spring vent) separately, and we combined estimates of vegetative cover and wet mass in this reach with data from vegetation surveys in the adjacent upper reach because both reaches were dominated by hydrilla (*H. verticillata*). Farther downstream, the middle reach was dominated by strap-leaf sagittaria (*Sagittaria kurziana*), with some eelgrass (*Vallisneria americana*), filamentous macroalgae, and *H. verticillata*. The lower reach was dominated by sand, with essentially no submersed aquatic vegetation. Water pennywort (*Hydrocotyle* spp.), duckweed (*Lemna valdiviana*), water lettuce (*Pistia stratiotes*), spring-run spider lily (*Hymenocallis rotata*), and watercress (*Nasturium* spp.) were present in the upper and middle reaches, but this emergent and floating vegetation was sparse.

Surveys

We surveyed turtles and vegetation across a total of 8097 m^2 during each of 2 sampling events (3 September and 4 October 2013) to document changes in vegetative cover, vegetative biomass, and number of turtles. Two observers counted turtles while snorkeling downstream along transects paralleling the shoreline in each of the 4 reaches.

Figure 1. Part of the aggregation of *Pseudemys concinna suwanniensis* that prompted this study of Blue Spring in Gilchrist County, Florida (USA). Photo by JMA.

Exceptional water clarity in Blue Spring, like other Florida springs (Duarte and Canfield 1990), ameliorated concerns regarding probability of detection during visual surveys. Transects varied in width because of the configuration of the spring run. The maximum width of an individual transect was 13 m. In each survey, we covered 8 transects (2/reach), and we traversed each transect 3 times.

We quantified submersed aquatic vegetation in the spring run along transects established perpendicular to the direction of flow at 25-m intervals in the upper and middle reaches of the spring run ($n = 7$ and $n = 6$, respectively). The absence of vegetation obviated the need for surveys in the lower reach. Along each transect, we estimated % cover for each taxon found in 3 haphazardly positioned quadrats (0.25 m^2). After estimating cover, we collected all aboveground biomass from each quadrat and placed it in a labeled bag. At the completion of a survey, we placed the bags on ice and transported them to the laboratory. In the laboratory, we separated taxa, drained excess water from each subsample, and weighed each subsample to the nearest gram to yield wet mass (WM) for each taxon. We calculated dry mass (DM) by applying previously established conversion factors (Politano 2008, TKF, unpublished data).

Statistical analyses and calculation of grazing rates

Changes in the abundance of turtles We analyzed numbers of turtles with a permutation analysis of variance (PERMANOVA; PRIMER, version 6; PRIMER-E, Plymouth, UK). In this analysis, we treated time (initial and final surveys) and reach (spring, upper, middle, and lower) as fixed factors, with transects nested in reaches. Given that multivariate permutation analyses of variance are sensitive to dispersion of data, we also conducted a permutation analysis of dispersion for each significant factor (PERMDISP; PRIMER).

Changes in submersed aquatic vegetation We analyzed data for % cover and WM for taxa that occurred in ≥2 quadrats in each of the 2 reaches with a PERMANOVA. In these analyses, time (1st and 2nd surveys) and reach (upper and middle) were treated as fixed factors, with transects nested in reaches. Again, we conducted a PERMANOVA of dispersion for each significant factor.

Grazing rates For taxa of submersed aquatic vegetation that exhibited significant differences in WM between surveys, we calculated daily per capita grazing rates using WM and converted the estimates to DM. We estimated grazing rates based on changes in WM in the reaches where a given taxon was common. To calculate changes in vegetative biomass, we scaled mean WM from the 2 surveys to WM/reach and subtracted the estimates of biomass from the 2nd survey from the appropriate estimates from the 1st survey. We used these changes to generate 3 grazing rates for each type of submersed aquatic vegetation. Grazing rates were calculated by dividing the change in vegetative biomass by the product of the number of days between the 1st and 2nd surveys (30 d) and either the mean, minimum, or maximum densities of turtles surveyed in the whole spring run (turtles traverse the whole spring run; Johnston et al. 2016). In addition, we converted grazing rates from WM to DM $turtle^{-1}$ d^{-1} for comparison to previous work.

RESULTS

Eleven turtle species occur in Blue Spring (Johnston et al. 2016), but we counted only *P. c. suwanniensis* >180 mm midline plastron length (i.e., subadult and adult females and males). These demographic categories made up ~93% of the aggregation, and the mean mass of each turtle was 4 kg (Johnston et al., in press).

Turtles exhibited a patchy distribution, which increased uncertainty surrounding estimates of density. Numbers of turtles declined significantly between the 2 surveys ($F_{1,4} = 4.13$, $p = 0.02$). In September 2013, we estimated a maximum mean density (±SE) of 421 ± 133 turtles/ha across all reaches, a value ~28× greater than the maximum density observed between 2003 and 2012 (Johnston et al., in press). Thirty days later, we recorded a mean density of 145 ± 58 turtles/ha among all reaches, a density ~9× greater than the previously recorded maximum (Johnston et al., in press). Numbers of turtles also varied significantly among transects ($F_{4,35} = 3.68$, $p < 0.01$), with a maximum mean density of 1566 ± 319 turtles/ha recorded across the 3 passes along a transect near the spring vent during the 1st survey. Neither of these significant differences was a result of increased variability among replicates as shown by nonsignificant tests for dispersion ($p > 0.05$ in both cases).

Three types of submersed aquatic vegetation occurred in ≥2 quadrats in both reaches, so they were included in PERMANOVAs. *Hydrilla verticillata*, *S. kurziana*, and *V. americana* had overall mean % covers of 30, 34, and 5%, respectively.

The analysis of % cover indicated significant variation in distribution of submersed aquatic vegetation among reaches when data were pooled across surveys ($F_{1,9} = 5.06$, $p = 0.03$). The analysis confirmed the a priori delineation of reaches, with *H. verticillata* covering more of the bottom in the upper reach (upper = 49 ± 6%, middle = 8 ± 3%), *S. kurziana* dominating cover in the middle reach (upper = 21 ± 4%, middle = 49 ± 6%), and *V. americana* more evenly distributed between the reaches and less common overall (upper = 3 ± 2%, middle = 7 ± 2%). The analysis also indicated a significant decrease in cover between the surveys across all reaches ($F_{1,9} = 3.80$, $p = 0.05$; Fig. 2A–C). Cover of *H. verticillata* was halved (40 ± 7% to 20 ± 4%), whereas decreases in the cover of *S. kurziana* and *V. americana* were smaller (35 ± 6% to 31 ± 5% and 6 ± 3% to 3 ± 1%, respectively). These significant variations were not the result of increased

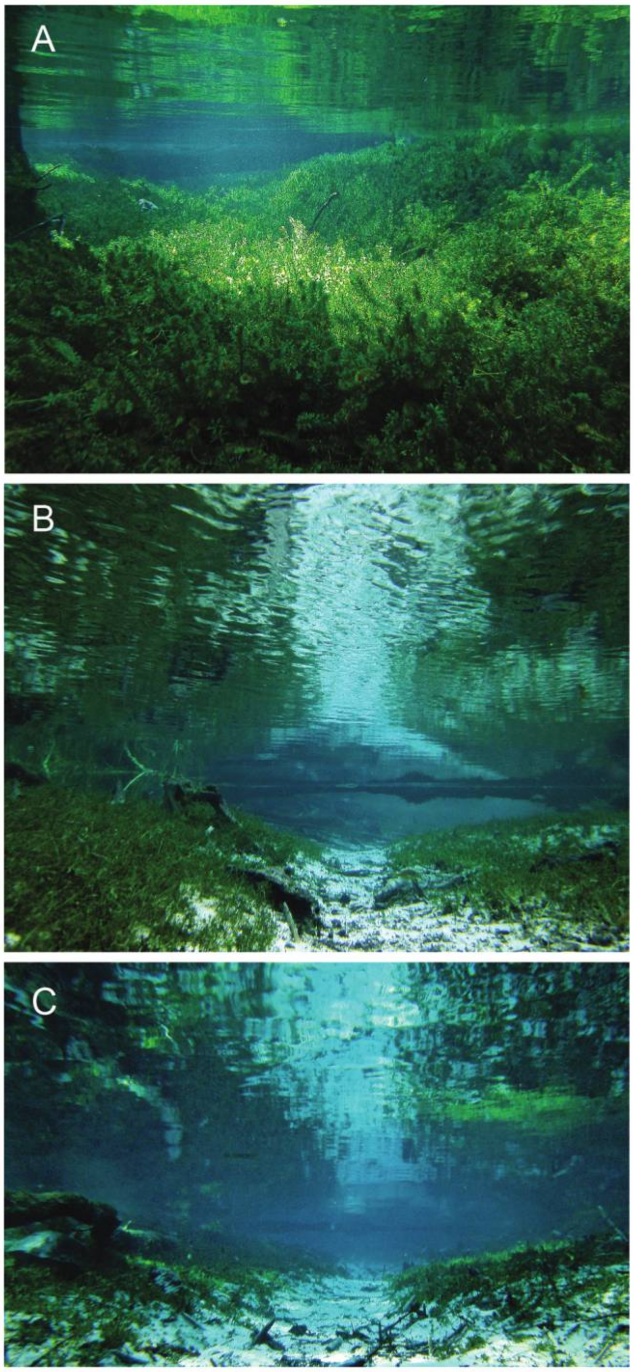

Figure 2. Appearance of vegetation, especially *Hydrilla verticillata*, before *Pseudemys concinna suwanniensis* aggregated (A), after turtles arrived and immediately prior to the first sampling event (B), and 1 wk after the first sampling event (C). Photos by JMA.

variation among replicates as shown by nonsignificant tests for dispersion ($p > 0.05$).

Percent cover was relatively consistent within a reach, but aboveground biomass was more variable, which led to uncertainty surrounding estimates of means. The analysis of WM yielded a more complex result than did the analysis of % cover, with a significant interaction between surveys and transects within reaches ($F_{9,56} = 1.51$, $p = 0.04$; Fig. 3A–C). The interaction can be elucidated by examining variation in the number of transects where decreases and increases in mean WM were observed. Decreases were noted for *H. verticillata* on 9 of the 10 transects where it occurred. Mean WM of *S. kurziana* decreased on 6 of 10 transects and WM of *V. americana* decreased on 5 of 6 transects. In addition, the magnitude of the changes in mean WM varied among transects. For example, the maximum decrease in mean WM was on transect 5 in the upper reach for *H. verticillata* (333 g), on transect 2 in the middle reach for *S. kurziana* (123 g), and on transect 3 in the middle reach for

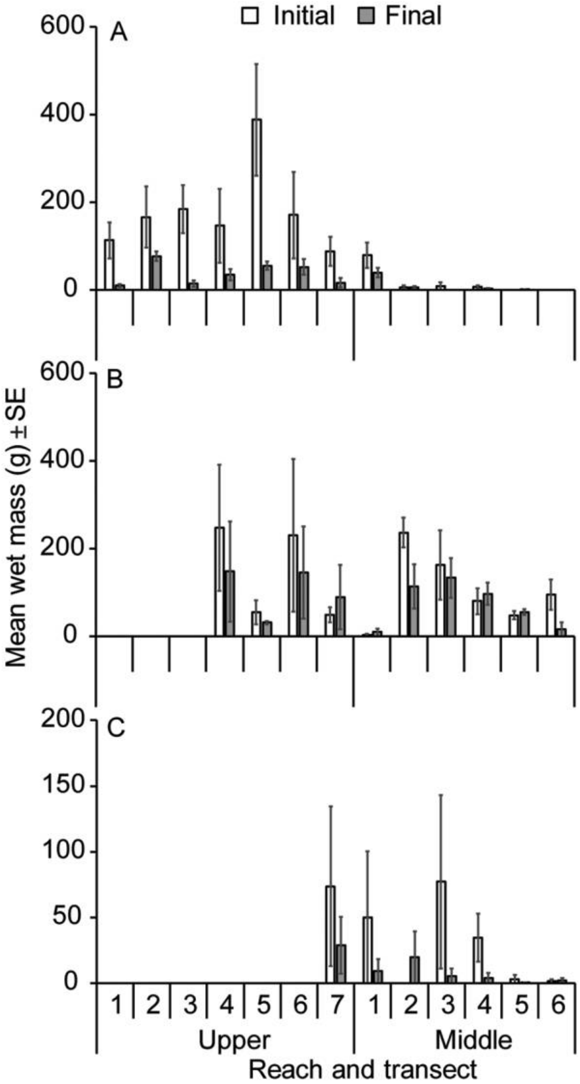

Figure 3. Mean (±SE) wet mass along transects in reaches during 2 surveys for *Hydrilla verticillata* (A), *Sagittaria kurziana* (B), and *Vallisneria americana* (C). Note the different *y*-axis scale in panel C.

V. americana (72 g). None of the significant differences was a result of increased variability among replicates ($p >$ 0.05 in all cases). Overall, WM decreased for all 3 aquatic plant species. We used these data to calculate grazing rates.

Observations and videos (Video S1) indicated that little vegetation was lost downstream as turtles grazed. Therefore, mean, minimum, and maximum grazing rates were based on mean losses of biomass scaled to the area of the appropriate reaches and mean, maximum, and minimum numbers of turtles in the complete spring run (Table 1). *Hydrilla verticillata* was grazed most heavily, whether quantified as change in WM or DM. *Hydrilla verticillata* was grazed 3× as heavily as *S. kurziana* and >10× as heavily as *V. americana*. *Sagittaria kurziana* was consumed 4–5× as heavily as *V. americana*.

DISCUSSION

The turtle aggregation in Blue Spring involved an extremely high density of adult and subadult *P. c. suwanniensis* (421 turtles/ha). Reports from elsewhere in Florida document densities between 3.3 and 42.8 turtles/ha (Huestis and Meylan 2004, Chapin and Meylan 2011, Johnston et al. 2011), with only 1 report of a density exceeding our maximum. A density of 741 turtles/ha was recorded in Fanning Spring (Jackson 1970), but that aggregation was dominated by juveniles, which suggests the spring served as a nursery. The exact cause of the aggregation we observed is uncertain, but we documented substantial feeding, which highlighted another reason spring habitats are important to this freshwater turtle.

At the time of our 1st sampling event, water level in the Santa Fe River was high (~7.0 m above National Geodetic Vertical Datum of 1929 [NGVD 1929]) and near flood stage (7.3 m above NGVD 1929; data from US Geological Survey station 02322500 near Fort White, Florida). Such high water probably affected *P. c. suwanniensis* in several ways. Energetic costs of swimming in the mainstem of the river probably increased, basking sites became scarce, and high concentrations of chromophoric dissolved organic matter, including tannins, potentially inhibited photosynthesis and growth of rooted vascular plants leading to reduced availability of food. Between surveys, water levels fell to 6.7 m above NGVD 1929, which may have combined with the dramatic decrease in available food (Fig. 2A–C) to result in the departure of turtles. Documenting how turtles use coupled riverine habitats will become increasingly important given the potential for flood events to become more frequent and extreme (IPCC 2014).

Calculated on a per capita basis, *P. c. suwanniensis* grazing rates on *H. verticillata*, *S. kurziana*, and *V. americana* were comparable to the only other available published values for turtles grazing on submersed macrophytes, i.e., *Chelonia mydas* (green sea turtles) feeding on *Thalassia testudinum* (Bjorndal 1980, Williams 1988; Table 2). *Pseudemys c. suwanniensis* consumed 3–5× more *H. verticillata* than *C. mydas* consumed *T. testudinum*, whereas grazing pressure exerted by *P. c. suwanniensis* on *S. kurziana* and *V. americana* was similar to that exerted by *C. mydas*. Mean grazing rates for *P. c. suwanniensis* feeding on *H. verticillata* were higher when scaled to body mass than when unscaled. In spite of the uncertainty surrounding estimates of turtle densities and plant biomass, we may have underestimated the effects of grazing if plant production between surveys was substantial. Future efforts to estimate grazing rates would be improved by more frequent counts of turtles, differentiation between removal and consumption of vegetation, and measurements documenting growth of vegetation.

Our results indicate that *P. c. suwanniensis* grazed invasive *H. verticillata* more heavily than the native macrophytes *S. kurziana* and *V. americana*. *Pseudemys c. suwanniensis* may serve as a natural control mechanism for nonnative plants in Florida's lotic systems. For example, in the Wakulla River, *P. c. suwanniensis* consumed another invasive macrophyte, *E. densa*, in significantly higher quantities than *S. kurziana* or *V. americana* (Lagueux et al. 1995). In addition, indices of relative importance derived from the volume and frequency of occurrence of *H. verticillata* and *V. americana* in the stomachs of *P. c. suwanniensis* captured in the spring-fed Withlacoochee River were >2× those for mats of filamentous algae and other forms of vegetation (Bjorndal et al. 1997). The Florida Fish and Wildlife Conservation

Table 1. Grazing rates for *Pseudemys concinna suwanniensis* feeding on submersed aquatic vegetation. Hyd = *Hydrilla verticillata*, Sag = *Sagittaria kurziana*, Val = *Vallisneria americana*, U = upper reach, M = middle reach, WM = wet mass, DM = dry mass, Mn = mean number of turtles across all reaches and both surveys, Min = minimum number of turtles derived from counts in all reaches during the final survey, Max = maximum number of turtles derived from counts in all reaches during the initial survey.

			Turtles (number/ha)			Grazing rate (g WM turtle^{-1} d^{-1})			Grazing rate (g DM turtle^{-1} d^{-1})		
Plant	Reach	Loss (g WM/ha)	Mn	Min	Max	Mn	Max	Min	Mn	Max	Min
Hyd	U	247,311	291	117	342	850	2115	722	68.3	170.0	58.1
Sag	U + M	80,131	291	117	342	275	685	234	25.3	63.0	21.5
Val	M	22,657	291	117	342	78	194	66	5.2	12.9	4.4

Table 2. Grazing rates for *Chelonia mydas* and *Pseudemys concinna suwanniensis* feeding on submersed aquatic vegetation. *Thalassia* = *Thalassia testudinum*, *Hydrilla* = *Hydrilla verticillata*, *Sagittaria* = *Sagittaria kurziana*, *Vallisneria* = *Vallisneria americana*, DM = dry mass, Mn = mean, Min = minimum, Max = maximum.

		Grazing rate (g DM turtle^{-1} d^{-1})					
Grazer	Plant	Mn	Max	Min	Grazer mass (kg)	Grazing rate (g DM kg^{-1} d^{-1})	Source
C. mydas	*Thalassia*	24			8	3	Bjorndal 1980
		82			30	3	
		177			48	4	
		218			66	3	
		30–220			<66	3[a]	Williams 1988
		127			26	5	
P. c. suwanniensis	*Hydrilla*	68	170	58	4	17	This study
	Sagittaria	25	63	22	4	6	
	Vallisneria	5	13	4	4	1	

[a] Calculation based on 220 g DM turtle^{-1} d^{-1} and 66 kg grazer mass.

Commission recommends removal of *H. verticillata* because of concerns over displacement of preferred vegetation (FWCC 2013). However, Bjorndal and Bolten (1993) provide evidence that *H. verticillata* is highly digestible and yields a high daily energy gain for *Pseudemys nelsoni* (Florida Red-bellied Cooter), and Fields et al. (2003) reported that *H. verticillata* in Texas lakes is one of the dominant foods for *Pseudemys texana* (Texas River Cooter). Thus, *H. verticillata* may represent a preferred food for *P. c. suwanniensis*, its congeners, and other freshwater turtles, but this hypothesis needs to be tested experimentally.

Our study highlights the role of turtles in freshwater food webs and the importance of springs as a habitat for turtles. Unfortunately, vegetation in many springs in Florida has shifted from native, rooted macrophytes to possibly less palatable, benthic, filamentous macroalgae, such as *Lyngbya* sp. (Bjorndal et al. 1997, Heffernan et al. 2010). The potentially detrimental effects of this shift on populations of *P. c. suwanniensis* and other freshwater turtles deserve further study.

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