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**Louise S. Venne · Joel C. Trexler ·
Peter C. Frederick**

Abstract Fire in uplands and wetlands results in a release of nutrients and increased light in the burned area. However, fire effects on aquatic community dynamics are not well understood. We hypothesized that the addition of light and nutrients resulting from prescribed burns in wetlands increases periphyton biomass and supports increased standing stock of marsh fishes. In the oligotrophic Everglades of Florida, USA, we conducted a 2×2 factorial experiment using prescribed burns over standing water (increased nutrients and light), mowing with removal of above-water vegetation (no nutrient increase), and shade houses (no light) to test the prediction that fire effects would lead to more periphyton biomass and greater abundance and size of fish compared to other treatments. We observed increased periphyton percent cover and biomass per area in response to fire treatments. Fish abundance showed a short-term increase in burned plots. Fish length, mass, and condition factor did not respond consistently to treatments, though some species responded to specific treatments. Wildfires in dry marshes that may combust organic soils and vegetation may impact wetlands more than prescribed burns in flooded marshes. Our study suggests that wetland fires can affect aquatic animal and plant community structure, at least for short periods post-fire.

Keywords Fire · Wetlands · Fish length · Everglades · Prescribed burn · Pulsed effects

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L. S. Venne (✉) · P. C. Frederick
Department of Wildlife Ecology and Conservation,
University of Florida, 110 Newins-Ziegler Hall,
Gainesville, FL 32611-0430, USA
e-mail: lvenne@ufl.edu

Present Address:
L. S. Venne
Amec Foster Wheeler, 1075 Big Shanty Rd NW,
Suite 100, Kennesaw, GA 30144, USA

J. C. Trexler
Department of Biological Sciences, Florida International
University, 11200 SW 8th Street, Miami, FL 33199, USA

Introduction

Fire is a naturally occurring disturbance in many upland and wetland ecosystems that, through combustion of vegetation, exposes the underlying substrate to light and redistributes nutrients important to primary production. In uplands, fire typically alters nutrient availability, increases nutritive content in post-fire vegetation, changes vegetative cover and structure, and influences animal use of the landscape (Whelan, 1995). Similarly, in wetlands, fire has been shown to remobilize nutrients (Smith et al., 2001; Qian et al., 2009), alter plant cover, structure, and composition (Smith & Newman, 2001), promote new

vegetative growth (Lugo, 1995) with enhanced nutritional content (Smith et al., 1984), and can influence aquatic bird use of the wetland landscape (Venne & Frederick, 2013). Many aquatic invertebrates respond to changes in vegetation post-burn by increasing biomass, density, and abundance (de Szalay & Resh, 1997; Munro et al., 2009; Beganyi & Batzer, 2011), possibly because of increased availability of food and alteration of microclimate (Hochkirch & Adorf, 2007). Most studies of the effect of fire on fish focus on montane watersheds, where sediment runoff negatively impacts water quality or reduced shading after a wildfire increases stream temperature (Gresswell, 1999). While a good understanding of how fire affects nutrient cycling and macrophytes in wetlands has been developed, the mechanisms and effect sizes of fire on periphyton, fish, and other aquatic consumers are less well understood.

Light is a key factor in determining primary production and composition of the algal assemblage (Mosisch et al., 2001). In temporary ponds and streams, more light increased algal biomass (Mosisch et al., 2001; Mokany et al., 2008), while less light resulted in decreased algal biomass (Hillebrand, 2005). Wetlands of the Everglades, USA, are characterized by very high productivity and standing stock of periphyton that grows in extensive mats over much of the landscape (Ewe et al., 2006; Gaiser et al., 2012). However, substantially less periphyton exists in sawgrass stands than in wet prairies and sloughs (McCormick et al., 1998). This is attributed to shading from dense macrophyte communities (Grimshaw et al., 1997; Thomas et al., 2006). While shading does not change composition of periphyton in the Everglades, high levels of shade (98%) can reduce gross photosynthesis and percent organic matter (Thomas et al., 2006).

Addition of limiting nutrients, such as phosphorus (P), initiate changes in algal biomass and shifts in species composition in aquatic systems (Mosisch et al., 2001), and this is particularly true in the extremely P-limited Everglades (Gaiser et al., 2011). Combustion by wildfire alters vegetation, possibly soil structure, and nutrient availability, typically resulting in increased bioavailability of P (Smith et al., 2001). In the Everglades, P is strongly limiting and remobilization of bioavailable P can be crucial for biota such as periphyton. In a P-dosing experiment, periphyton biomass increased within 18 days at doses of 32 mg

$P/m^2/wk$ (McCormick & Scinto 1999). This suggests that even small and temporary pulses of nutrients from a fire in an oligotrophic wetland may affect primary production.

An increase in periphyton biomass can provide more food resources to consumers depending on species composition of the periphyton mat (Rader & Richardson, 1992; Geddes & Trexler, 2003). Many algal species employ protective mechanisms (e.g., toxins, calcite encrustation) to avoid herbivory, thereby affecting edibility of the periphyton mat. Increased algal biomass resulted in a shift in the community of consumers from filter feeders to algal grazers in temporary ponds (Mokany et al., 2008). Similarly, periphyton rich in green algae and diatoms is a preferred food for wetland herbivores (McCormick & Scinto, 1999), and areas relatively rich in these algae support higher biomass of many aquatic consumers (Browder, 1981; Sargeant et al., 2011). Thus, a pulse of nutrients and increase in light, such as results from fires, may alter algal species composition sufficiently to affect the aquatic consumer community, including species of fish and macroinvertebrates that serve as links to higher trophic levels. The direction of shift appears to depend on the species composition of periphyton affected, and the community of grazers.

We conducted a field experiment in which we manipulated light and nutrients through burning, mowing, and shading in order to determine how fire may affect wetland primary production and fish standing stock. We predicted that (1) an increase in light and nutrients would result in more periphyton biomass and cover and (2) an increase in periphyton biomass would increase total and individual fish size, condition factor, and relative abundance.

Materials and methods

The Everglades is a large, oligotrophic, P-limited wetland in southern Florida, USA (Noe et al., 2001). Sawgrass (*Cladium mariscus* [L.] Pohl ssp. *Jamaicense* [Crantz] Kük) is the dominant vegetation in the freshwater marsh and forms large, slightly elevated "ridges" surrounded by deeper open water sloughs that contain periphyton mats, submerged aquatic vegetation, and some emergent vegetation (Gunderson, 1994). Sawgrass is a fast-growing, fire-adapted plant with senescent leaves retained on the

margins of the culm. Sawgrass stands typically recover within 2 years post-burn (Wade et al., 1980). This growth form, coupled with a high frequency of lightning, promotes fire (Wade et al., 1980), resulting in a wetland system that historically burned frequently, primarily at the onset of the wet season (Gunderson & Snyder, 1994; Slocum et al., 2007). During severe droughts, fires that burned the peat may have been common and likely increased with drainage of the Everglades (McVoy et al., 2011).

As part of a management plan to mimic natural fires, the Florida Fish and Wildlife Conservation Commission conducted a prescribed burn on 01 April 2010. We used this controlled burn to study the effects of fire. The burn unit was approximately 690 ha and incorporated approximately 70% sawgrass, 25% slough, with woody tree islands, cattail (*Typha* spp.), and willow (*Salix* spp.) composing the remainder. Approximately 45% of the overall fuel density was considered heavy. The fire was conducted over standing water ($\bar{x} = 17.5$ cm deep) and was a complete burn, leaving sawgrass and buttonbush (*Cephalanthus occidentalis* L.) stubble standing approximately 32 cm above the water surface, typical of burns over standing water in the Everglades.

From 01 April to 04 April, 2010, we set up a 2×2 factorial experiment in which we manipulated nutrients and light in 20 10-m $\times$ 10-m plots in sawgrass ridges. Five treatments were assigned randomly to pairings of plots within the planned burn unit and nearby unburned area: burned (nutrients and light added through fire—hereafter named "Nutrients + Light"), burned with shade house (nutrients added through fire, but no light—"Nutrients Only"), mowed with removal of above-water vegetation (no fire, no nutrients, light added—"Light Only"), mowed with removal of above-water vegetation and shade house (no fire, this treatment served as a control with no nutrients and no light added—"No Nutrients or Light"), and unmanipulated sawgrass with ambient light (not burned, "Experimental Control"). Burned treatments were considered nutrient augmented via ash from the burn (e.g., Liu et al., 2010), and plots without nutrients were mowed, and the mowed vegetation was removed (light treatments). This is based on the assumptions that a fire temporarily increases concentrations of available nutrients and that mowing with removal of above-water vegetation would mimic the typical increase in light following

burns but not add nutrients. Artificially shaded treatments were plots with and without shade houses to mimic natural shading from sawgrass. Shade cloth was selected using light levels measured for photosynthetically active radiation (PAR) using an AccuPAR LP-80 (Decagon Devices, Pullman, WA) in sawgrass at five locations in sawgrass stands in the study area (63–95% shading, $\bar{x} = 84 \pm 12\%$, $n = 6$). We added the fifth treatment in a stand of unmanipulated sawgrass as an Experimental Control since the control treatment ("No Nutrients or Light") in the 2×2 factorial design was mowed and shaded. "No Nutrients or Light" plots served as a control for the treatment process and benchmark for ambient conditions, so we refer to this fifth treatment as "Experimental Control."

Burned plots (i.e., "Nutrients + Light" and "Nutrients Only") were located within the sawgrass ridges (>1 ha) of the large prescribed burn. This increased the likelihood that burn effects were representative of the management tool and minimized edge effects and mimicked the intensity and fire effects of large burns. We used ArcMap (Esri, Redlands, CA) to randomly select eight points, four in the prescribed burn unit, and four in an adjacent unburned area, from which bearings were randomly selected to place plot locations in the next nearest, sufficiently large (>1 ha) sawgrass ridge. Plots were positioned in sawgrass 30–45 m from the edge of the ridge to reduce edge effects. We mowed an area of 12 m $\times$ 12 m with articulating hedge trimmers to a vegetation height above the marsh surface approximately equivalent to burned vegetation ($\bar{x} = 47.5$ cm). We moved the mowed vegetation to sloughs >50 m away and downstream from any plots. The extra area (10 m plots vs. 12 m mowed) was mowed to reduce refuge for aquatic organisms in standing sawgrass on the edge of the plots. On the day following vegetation removal (burned or mowed), within plots, we constructed 10 m $\times$ 10 m $\times$ 2 m (l $\times$ w $\times$ h) shade houses of 80% spectrally neutral black knitted cloth (International Greenhouse Company, Danville, IL, USA) in shaded plots. We also mock disturbed light treatments that did not get shade houses since the shade house plots were trampled by research personnel during set-up. "Experimental Control" plots were not trampled.

We collected water samples for analysis of phosphorus from nutrient treatment plots in the morning before the burn occurred, in the afternoon shortly after the burn was completed (day 1), and on days 2, 3, 5, 7,

9, 12, and 15. Samples in nutrient treatments were collected within 5 m upstream of plots to avoid influence of the shade house set-up on P concentrations. Given no apparent mechanism for P release, we assumed that mowing treatments would not elevate P concentrations, and did not collect water samples in these treatments as frequently as in burned treatments. We collected water samples in the no-nutrient treatments (i.e., Light Only, No Nutrients or Light) within 0–3 days prior to treatment, immediately after mowing (labeled day 0.5 if a shade house was constructed the following day to complete the treatment), and 1 day after setting up the treatment, and in two "Experimental Control" sites the morning before the burn and on day 5 post-burn. If a P increase were to result from mowing, this would be captured within the first day after treatment by the sampling regime.

Water samples were placed on ice and processed the evening of the day sampled. We transferred and acidified 40 mL of sampled water to analyze for total phosphorus (TP) and filtered and acidified 40 mL of sampled water to analyze for soluble reactive phosphorus (SRP). Samples were kept at 4°C and analyzed by the National Environmental Laboratory Accreditation Program (NELAP)-certified University of Florida Wetland Biogeochemistry Laboratory (Gainesville, FL) within 2.5 months of collection. Additionally, at all water sample locations, we collected large clumps of periphyton (<1 l), where present, prior to and immediately after the prescribed burn. These samples were ashed and analyzed for TP at the University of Florida Wetland Biogeochemistry Laboratory.

We sampled treatment plots for biotic responses once every 10 days starting 2 days after all plots were set up, for a total of eight sampling periods from early April to the end of June 2010. In all plots, we measured water depth, average, and maximum vegetation height, and we haphazardly placed a 0.25-m^2 quadrat to estimate percent vegetation cover, percent periphyton cover, and percent periphyton collected (for Chlorophyll *a* analyses). Percent periphyton cover was visually estimated as percent of marsh bottom, vegetative material in water column, and water surface covered by periphyton. The periphyton we collected was stored in plastic bags on ice and transferred to a −20°C freezer within 7 h of collection.

We sampled the fish assemblage using minnow traps to record the relative catch-per-unit-effort (CPUE) for each plot. In each plot, we set 3 Gee minnow traps (23 × 45 cm, 3.2 mm mesh, Memphis Net & Twine Co., Inc., Memphis, TN) for 2 h. After 2 h, we removed the traps, euthanized, and preserved the animals collected in formalin for later processing in the laboratory. Fish were euthanized by emersion in MS-222 in the field following standard protocols for humane treatment of fish in research (Anonymous, 1988). In the laboratory, we identified and measured total length (TL ± 1 mm) and mass (±0.1 g) of each aquatic organism captured. We used standard equations relating TL to standard length (SL) for individual fish species (Kushlan et al., 1986; Klassen et al. 2014) to convert measurements. Encounter sampling devices such as minnow traps yield CPUE information that may be biased among species. CPUE depends on animal activity and density, and capture efficiency varies among species and size classes (e.g., Blaustein, 1989; He & Lodge, 1990; Layman & Smith, 2001; Obaza et al., 2011). For species with consistent activity levels and capture efficiency among treatments, minnow traps can provide an accurate index of abundance (He & Lodge, 1990). While throw traps would be a more accurate way to estimate abundance and standing stock, the methodology requires removal of all vegetation and roots. This would have changed the habitat and treatment effects in the plots almost immediately and with increasing severity over the course of the study (Loftus & Eklund, 1994). During the last sampling period (approximately 90-d post-treatment), we also used 1-m^2 throw traps to sample all mowed and burned plots. We threw two traps in each plot, cleared traps following methods of Jordan et al. (1997), and measured TL of the organisms captured. We compared the throw trap density estimates to minnow trap CPUE estimates to evaluate the assumption of consistent minnow trap collection efficiency across treatments.

We measured PAR in three locations in each plot once per month between April and June, 2010. Readings were taken between 1000 and 1400 h (to minimize variation due to the sun azimuth) every minute for 15 min. Readings at all locations in each plot were pooled and averaged to calculate percent shading in the plots.

Periphyton samples were analyzed for Chlorophyll *a* following the methods of Sartory and Grobbelaar (1984) at a NELAP-certified University of Florida laboratory (Gainesville, FL). A small (∼20 mg, wet

weight) subsample of periphyton was weighed and processed, while the remaining periphyton from each plot was used to determine wet:dry weight ratios to calculate periphyton biomass. From this, we calculated corrected Chlorophyll a (μg/g) and periphyton mass (g) on a dry weight (dw) basis per area (m^2).

We tested normality of environmental variables (vegetation variables, water depth, and percent shading) with a Shapiro–Wilk normality test. For percent periphyton cover, average and maximum vegetation height and percent vegetation cover, a transformation did not achieve normality, so we rank transformed the data and analyzed for differences among treatments using Kruskal–Wallis rank-sum tests. We analyzed water depth, percent vegetation cover, and percent shading with an analysis of covariance (ANCOVA) using sampling period as the covariate. For TP and SRP, we compared daily concentrations post-burn to concentrations pre-burn using paired Wilcoxon signed-rank tests.

Fish richness and Shannon–Wiener diversity indices were not normally distributed so data were rank transformed and analyzed for differences among treatments using Kruskal–Wallis rank-sum tests. We analyzed fish metrics (standard length, mass, condition factor, abundance, and relative abundance) for species that were caught in at least 80% of plot-sampling period combinations. We analyzed all species combined and individual species using generalized least squares (*gls*) in R (R Development Core Team, 2009). Due to repeated sampling of the same plots, we used models incorporating autoregressive variance–covariance structure and compared models with and without the assumption of heterogeneous variances to determine if there were significant differences among treatments or between sampling periods. We inspected histograms of the residuals and plots of the residuals versus predicted values to determine if transformation was necessary. If there was a significant difference among treatments, we set up three contrasts to compare "Experimental Control" versus treatments, light versus no light, and nutrients versus no nutrients. To maintain orthogonality of the contrasts, we omitted the "Experimental Control" treatment from the latter two contrasts. Additional, orthogonal contrasts were included based on potential response times of the periphyton and fish community, to determine if a pulse, rather than a sustained elevation of productivity occurred after treatment. Contrasts we included were

specific to the sampling periods, period 1 versus 2–8 (i.e., immediate response to burn and nutrient release), 1–3 versus 4–8 (i.e., response to potential periphyton growth responding to nutrient pulse), and 1–4 versus 5–8 (i.e., response related to periphyton and aquatic organisms responding to burn and nutrient pulse). Based on a graphical inspection, a contrast of Nutrients + Light and periods 2 and 3 versus 1 combined with 4–8 was performed post hoc.

Relative abundance of fish was organized into a species × site matrix. We fourth-root transformed relative abundance to reduce the weight of dominant species on more rare species. We conducted a permutational multivariate analysis of variance using distance matrices (PERMANOVA; Anderson, 2001) for this community matrix, using 999 permutations and Jaccard's coefficient to calculate distances for relative abundance using the *adonis* function in R package *vegan* (Oksanen et al., 2015). Permutations were limited to within each period since there were significant differences among some periods and response variables.

Results

Nutrients

Immediately following completion of plot treatments, TP concentrations in water collected in nutrient (i.e., burned) treatments increased ($F = 12.2$, $df = 1$, $P < 0.001$) with concentrations in the nutrient treatments as high as 0.161 mg/L ($\bar{x} = 0.077$ mg/l; Fig. 1), an approximately order of magnitude increase from pre-burn TP concentrations, confirming our expectation of increased nutrients in burned plots. However, the average concentration dropped to 0.024 mg/l (max. = 0.053 mg/l) the day after the burn (day 2). TP concentrations leveled off at approximately 0.014 mg/l, remaining significantly greater than the average pre-burn TP concentration (0.008 mg/l). On day 5, nutrient plot TP concentrations were elevated to 0.034 mg/l after concentration had declined from the initial peak. On day 15, in nutrient plots TP concentrations dropped to 0.005 mg/l, lower than pre-burn concentrations. Concentrations in the no-nutrient (i.e., mowed) and "Experimental Control" treatments were not significantly different than pre-treatment TP concentrations on any day.
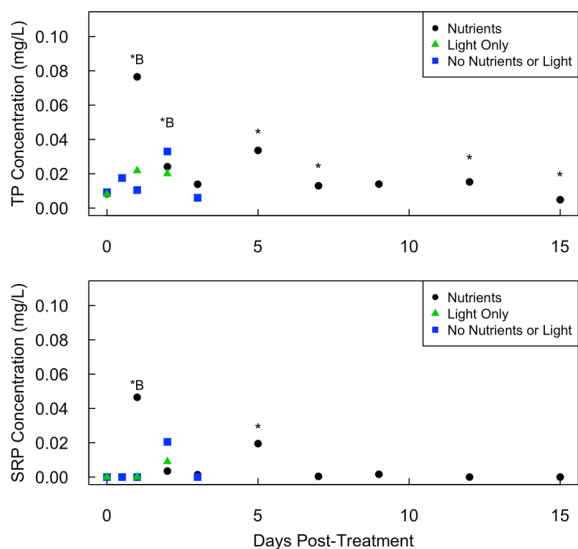
Fig. 1 Concentrations of total phosphorus (TP) and soluble reactive phosphorus (SRP) in water sampled collected pre-burn (day 0) and post-burn (days 0.5–15) in nutrient plots (burned), "Light Only" (mowed with vegetation removed), and "No Nutrients or Light" (mowed with vegetation removed and a shade house constructed) in northern Water Conservation Area 3A South of the Everglades, Florida, USA. *B indicates that concentration in burn on that day is significantly different than pre-burn phosphorus concentration. All other samples were not significantly different from pre-burn phosphorus concentrations

SRP concentrations in nutrient (i.e., burned) treatments spiked ($F = 6.64$, $df = 1$, $P = 0.012$) immediately post-treatment to an average of 0.047 mg/L (max. = 0.163 mg/l; Fig. 1). SRP concentrations returned almost to detection limits the following day ($\bar{x} = 0.003$ mg/l, max. = 0.013 mg/l) and remained low thereafter with the exception of day 5, corresponding with a spike in TP concentrations, when SRP concentrations were elevated to 0.020 mg/l. SRP concentrations in the no-nutrient and "Experimental Control" treatments were not significantly different than pre-treatment concentrations on any day.

Other physical factors

Water depth was approximately 3 cm shallower in the "Nutrient Only" treatment plots compared to the no-nutrient (i.e., mowed) treatments ($F = 5.48$, $df = 4$, $P < 0.001$), but water depth did not vary substantially over the course of the experiment (Table 1; $F = 1.22$, $df = 1$, $P = 0.270$), and the interaction of treatment and sampling period was not significant ($F = 1.59$,

$df = 4$, $P = 0.181$). Following manipulation, all treatments were different in percent shading ($F = 12$, $df = 4$, $P < 0.001$) from each other except the "No Nutrients or Light" and "Nutrients Only" (i.e., shaded) treatments, "Experimental Control" and "Light Only" treatments, and "Nutrients + Light" and "Light Only" treatments, indicating that the intended shading treatment was effective. Percent vegetation cover did not differ among treatments over the course of the experiment; however, average and maximum vegetation heights were 2–3 times higher in Experimental Control than all other treatments (Tables 1, 2). Vegetation grew over time, where changes in height were driven predominantly by the manipulated plots ($t = 9.065$, $df = 1,125$, $P < 0.001$, adjusted $R^2 = 0.39$; excluding the "Experimental Control" treatment).

Periphyton

Percent periphyton cover was approximately two times greater in the "Nutrients + Light" treatment than in all other treatments (Tables 1, 2). The treatments with the lowest percent periphyton cover were the "Nutrients Only" and the "No Nutrients or Light." Similarly, on a dry weight (dw) basis, periphyton mass per area was approximately three times greater in the "Nutrients + Light" treatment than in all other treatments, while the treatment with the lowest periphyton mass per area was "No Nutrients or Light." Concentrations of chlorophyll *a* were not different among treatments.

Overall fish metrics

The CPUE of fish (sum of all species) was approximately 71% greater in the "Nutrients + Light" treatment compared to the "No Nutrients or Light" treatment but did not differ from the other treatments (Table 1). Overall fish mass, length, condition factor, relative abundance, and richness were not different among treatments (Tables 1, 2). Diversity of fishes was approximately 16% greater in treatments with light than the no-light and Experimental Control treatments and approximately 5% lower in the "Experimental Control" and "No Nutrients or Light" than the other treatments (Tables 1, 2).

We captured 10 species of fish, 2 species of invertebrates, 3 species of amphibians, 1 species of

Table 1 Mean (±standard deviation) of environmental variables measured post-treatment in plots in sawgrass stands manipulated with fire, mowing, and shading in the central Everglades of Florida, USA

Variable	Experimental Control	No Nutrients or Light	Light Only	Nutrients Only	Nutrients + Light
Water depth (cm)*	17.1 (3.6)[bc *]	17.3 (3.1)[c]	19.3 (3.8)[c]	15.2 (3.1)[ab]	17.4 (3.9)[bc]
Shading (%)*	63 (27)[b]	89 (4)[a]	36 (26)[c]	87 (6)[a]	50 (18)[bc]
Median vegetation height (cm)*	165[a]	71[c]	83[b]	69.5[c]	89[b]
Vegetation height range (cm)	142–215	37–103	27–122	39–98	32–120
Median max. vegetation height (cm)*	200[a]	101 [cd]	114[b]	94.5[d]	104[bc]
Max. vegetation height range (cm)	161–350	51–150	56–177	56–175	43–157
Vegetation cover (%)	40.7 (28)	27.8 (19)	29.0 (22)	26.3 (9.4)	25.3 (18)
Periphyton cover (%)*	21.4 (24)[b]	8.1 (14)[c]	13.5 (14)[b]	11.3 (14)[c]	26.6 (23)[a]
Periphyton mass per area (g dw/m^2)*	41.5 (65)[b]	2.8 (5.4)[c]	12.5 (26)[b]	8.6 (14)[b]	50.5 (83)[a]
Average chlorophyll a (µg/g dw)	558 (630)	771 (543)	687 (387)	1084 (920)	689 (366)
Chlorophyll a (µg/g dw)	0–2134	0–2486	0–1474	0–3590	0–1400
Average fish standard length (mm)	26.1 (4.6)	26.2 (2.6)	26.5 (2.7)	27.3 (2.9)	27.0 (2.9)
Average fish mass (g)	0.54 (0.36)	0.52 (0.22)	0.56 (0.23)	0.59 (0.26)	0.56 (0.24)
Average fish condition factor	2.01 (0.17)	2.07 (0.18)	2.12 (0.25)	2.04 (0.16)	2.05 (0.19)
Average fish CPUE	48.7[ab]	37.3[b]	55.4[ab]	50.2[ab]	63.8[a]
Average relative CPUE	20.4	20.6	17.4	18.6	18.0
Richness	4.9 (1.5)	4.8 (1.2)	5.7 (1.2)	5.4 (1.2)	5.5 (1.2)
Shannon diversity*	1.09[bc]	1.03[c]	1.27[a]	1.03[c]	1.17[ab]

Treatments were Nutrients + Light (nutrients and light added through fire), Nutrients Only (nutrients added through fire, but no light due to shading from shade house), Light Only (no fire, no nutrients, but light added due to mowing with removal of above-water vegetation), No Nutrients or Light (no fire, mowing with removal of above-water vegetation and shade house; this treatment served as a control with no nutrients and no light added), and Experimental Control (not burned or mowed, unmanipulated sawgrass with ambient light)

* Significant difference among treatments; differences were denoted by different letters (e.g., Result[a] differs from Result[b]). Summary of statistical results is provided in Table 2 or in text

reptile, and 2 species of crustaceans in minnow traps (Table 3). Four species of fish (eastern mosquitofish [*Gambusia holbrooki* Girard], least killifish [*Heterandria formosa* Girard], flagfish [*Jordanella floridae* Goode and Beane], sailfin molly [*Poecilia latipinna* Lesueur]) were captured in nearly all plots during the study. Three of the fish species (Everglades pygmy sunfish [*Elassoma evergladei* Jordan], redfin pickerel [*Esox americanus* Gmelin], and spotted sunfish [*Lepomis punctatus* Valenciennes]) were captured very infrequently (captured 1, 2, and 11 times, respectively, out of 160 possible plot-period combinations).

Flagfish, sailfin mollies, and least killifish captured in minnow traps showed differences among treatments (Table 5). Flagfish in "Experimental Control" treatments were smaller (approximately 2 mm shorter and 0.1 g lighter) and had approximately 78% lower relative abundance than the combined mean of all other treatments (Tables 4, 5). Additionally, flagfish were bigger (approximately 2 mm longer and 0.2 g heavier) in no-nutrient treatments compared to nutrient treatments. We caught approximately 5 more flagfish per capture event in light treatments than in no-light treatments. Sailfin mollies were almost 0.2 g

Table 2 Summary of responses of biotic variables to treatments (Kruskal–Wallis rank-sum test)

Variable	Treatment		P
	df	χ^2	
Periphyton			
Periphyton cover (%)	4	16.7	0.002*
Periphyton mass per area (g dw/m^2)	4	18.7	0.001*
Chlorophyll a (corrected) (µg/g dw)	4	7.04	0.134
Vegetation			
Vegetation cover (%)	4	6.12	0.190
Vegetation height (cm)	4	83.6	<0.001*
Maximum vegetation height (cm)	4	76.5	<0.001*
Fish			
Richness	4	9.30	0.054
Diversity	4	11.6	0.021*
Relative abundance	4	5.95	0.203

* Significant P value ($P < 0.05$)

dw dry weight

heavier in no-nutrient treatments compared to nutrient treatments (Tables 4, 5). Least killifish were approximately 0.5 mm (almost 3%) longer in no-light treatments than light treatments and approximately 7% (about 1 mm) longer in nutrient treatments than no-nutrient treatments (Tables 4, 5). Least killifish had approximately 65% greater relative abundance in "Experimental Control" plots than in treatment plots. Relative abundance of least killifish in no-nutrient treatments was approximately two times greater than in nutrient treatment plots. Eastern mosquitofish showed no differences among treatments (Tables 4, 5).

Temporal effects were also apparent in this experiment. Additional contrasts indicated that CPUE was approximately 33% lower during the first sampling period than the remaining 7 periods. In the first three sampling periods, CPUE was greater in the manipulated plots than in the "Experimental Control" plots by approximately 1 unit CPUE. The post hoc contrast of "Nutrients + Light" against the other treatments and sampling periods 2–3 against periods 1 and 4–8 indicated that abundance was approximately two times greater (96%) in the "Nutrients + Light" treatment during periods 2–3 compared to the other treatments combined during periods 2–3 and compared to the other treatments combined during periods

1 and 4–8. However, "Nutrients + Light" was not significantly different from the other treatments across all periods and periods 2–3 were not significantly different from periods 1 and 4–8 across all treatments.

During the final sampling period, throw traps were also used to sample plots in order to quantify fish density in manipulated plots. Fish density in throw traps was approximately 60% greater in light than in no-light plots (Table 4). There were no differences associated with nutrient treatments (Table 4). Standard length of all fish and individual species of fish caught in throw traps did not differ among treatments with the exception of the Everglades pygmy sunfish and marsh killifish (*Fundulus confluentus* Goode and Bean; Table 4). The Everglades pygmy sunfish captured using throw traps were approximately 20% longer in light than no-light treatments while marsh killifish were almost 40% longer in nutrient treatments than no-nutrient treatments (Tables 4, 5). However, there was a significant interaction between light and nutrients for marsh killifish length, where lengths under conditions of light were greater in "Nutrients + Light" than in "Light Only" plots, but lengths in no-light treatments were similar between "Nutrient Only" and "No Nutrients or Light" treatments. CPUE of minnow traps and density of fish in throw traps were correlated in this final period ($r = 0.554$, $P = 0.026$).

Fish community response

We used community dissimilarity matrices of relative abundance to determine if treatments had an effect on the fish community sampled. While p-values indicated significant ($P < 0.001$) treatment and period main effects but not the interaction of these variables, the partial R^2 statistic was low ($R^2 \leq 0.107$). This result indicates that relative abundance of fish communities sampled differed among treatments and periods, but the strength of the relationship of the fish community to the particular treatments and periods was limited. The inclusion of crustaceans (i.e., riverine grass shrimp (*Palaemonetes paludosus* Gibbes*) and crayfish (*Procambarus* spp.)) did not change results.

Discussion

We found that nutrient-related effects of burning were rapid and relatively short-lived. Following burning, P

Table 3 Frequency of capture of aquatic organisms in minnow traps by treatment plot and species in the Everglades, 2010

Species	Experimental Control[a]	No Nutrients or Light	Light Only	Nutrients Only	Nutrients + Light
Fish					
Elassoma evergladei (Everglades pygmy sunfish)	0	0	0	1	0
Esox americanus (redfin pickerel)	0	0	2	0	0
Fundulus chrysotus Günther (golden topminnow)	18	11	16	25	24
F. confluentus (marsh killifish)	21	23	27	34	25
Gambusia holbrooki (eastern mosquitofish)	32	32	32	31	32
Heterandria formosa (least killifish)	28	29	31	19	23
Jordanella floridae (flagfish)	23	28	31	31	31
Lepomis punctatus (spotted sunfish)	2	2	1	3	3
Lucania goodei Jordan (bluefin killifish)	8	4	16	9	16
Poecilia latipinna (sailfin molly)	25	26	28	25	24
Crustaceans					
Palaemonetes paludosus (riverine grass shrimp)	18	19	23	14	21
Procambarus spp. (crayfish)	10	18	13	9	5
Herpetofauna					
Nerodia fasciata Linnaeus (Florida water snake)	2	1	0	1	1
Notophthalmus viridescens piaropicola Schwartz and Duellman (peninsula newt)	0	0	1	0	0
Siren lacertina Österdam (greater siren)	1	1	0	0	1
Lithobates grylio Stejneger (pig frog)	3	3	3	0	3
Macroinvertebrates					
Belastomatidae (giant water bug)	1	0	0	2	1
Dytiscidae (predaceous diving beetle)	6	3	1	5	9

[a] Number of plot and period combinations in which each species was captured at least once. Total possible plot and period combinations per treatment is 32

concentration was initially elevated in the water column, but for a very short time; P elevation in periphyton rapidly followed the spike in water column P, and we believe that uptake by benthic, water column, and periphyton microbial and algal communities was probably responsible for the quick decrease in fire-mobilized P. Fish response was varied, but abundance increased in the burn treatment ("Nutrients + Light") approximately 3–4 weeks after treatment for a short period and then was indistinguishable from the other treatments. This macro-faunal response suggests that the P release from fire had a traceable, but very short-lived, effect through the trophic web.

Post-burn TP and SRP concentrations in water spiked approximately an order of magnitude above pre-burn concentrations for less than 24 h, indicating that nutrient availability to biota is short-lived after aboveground fire in the Everglades. Similarly, post-

burn P concentrations in nutrient-enriched, cattail-dominated areas of the Everglades spiked relatively quickly and then dropped to pre-burn concentrations (Miao et al., 2010) although at slower rates than in the sawgrass dominated marshes sampled in this study. Absorption by periphyton was likely the primary mechanism for decreasing concentrations of P following the spike on day 1 post-burn (Noe et al., 2001; Saiers et al., 2003). Periphyton readily uptakes P, in accordance with the loading rate and duration that P is available (Newman et al., 2004). In two periphyton samples we collected at the same site pre- and immediately post-burn, periphyton tissue P concentrations increased by 0.027 and 0.073 mg/kg TP to 0.205 and 0.236 mg/kg, respectively. This elevation in periphyton P concentration reflected P concentration increases in water immediately post-burn at the same sites (0.036 and 0.040 mg/l TP, respectively). Thus,

Table 4 Mean (±standard deviation) of density (no. individuals m^{-2}) and length of fish captured in 1-m^2 throw traps with summary of response of throw trap results to light (light vs. no-light) and nutrient (nutrient vs. no-nutrient) treatments

Variable	No Nutrients or Light	Light Only	Nutrients Only	Nutrient + Light	Light		Nutrients		Interaction		df[a]
					F	P	F	P	F	P	
Density*	17.1 (4.8)	36.0 (17.1)	23.4 (9.6)	29.3 (9.2)	4.98	0.046*	0.002	0.965	1.37	0.264	12
Standard length (mm)											
All fish[b]	16.7 (7.8)	16.4 (6.9)	18.5 (10.2)	14.9 (4.3)							
E. evergladei*	14.3 (1.0)	17.0 (2.1)	11.4 (1.2)	15.1 (4.4)	6.33	0.024*	4.64	0.048*	0.170	0.686	15
F. chrysotus[b]	22.3 (15.8)	11.1	44.3	13.5 (2.2)							
F. confluentus*	15.8 (2.5)	11.7 (4.5)	16.5 (2.3)	22.7 (3.0)	0.152	0.706	14.6	0.004*	5.42	0.045*	9
G. holbrooki	14.0 (2.7)	12.2 (3.5)	12.8 (3.1)	13.8 (2.9)	0.189	0.667	0.106	0.747	2.17	0.152	27
H. formosa	11.1 (0.85)	11.5 (0.90)	12.0 (1.4)	12.0 (0.93)	0.249	0.622	3.24	0.083	0.203	0.656	28
J. floridae	22.0 (8.5)	29.7 (5.9)	23.9 (8.9)	17.1 (5.7)	0.309	0.585	2.99	0.100	4.99	0.038*	19
L. goodei	–	15.5 (6.3)	16.9 (1.5)	14.9 (3.8)	0.733	0.417	0.008	0.933		NA	8
L. punctatus	–	27.2	48.3 (9.4)	–			NA				
P. latipinna[c]	22.9 (9.5)	20.7 (6.6)	19.6 (3.1)	13.2 (1.4)	3.36	0.081	3.78	0.065	1.67	0.210	21

* Significant difference among treatments, ANOVA

[a] Degrees of freedom (denominator) for light, nutrients, interaction, and residuals, respectively. Where no standard deviation is provided, a single sample was captured. Numerator degrees of freedom are 1

[b] "All fish" and *F. chrysotus* were not normally distributed and were analyzed for differences between light and between nutrient treatments using a Kruskal–Wallis rank-sum test. *P* values were >0.21 and are not reported

[c] *P. latipinna* standard lengths were log-transformed to meet assumptions of normality

– Indicates the species was not caught in that treatment

NA Indicates ANOVA was not conducted due to small sample size

fire appears to be an important, if ephemeral, process for remobilizing P and probably makes P readily available to biota at the base of the aquatic trophic web.

Phosphorus in water can also diminish by flowing out of the burn, but this is not likely the primary mechanism for our study site. P flow post-burn has been detected at least 100 m downstream of burns (Miao et al., 2010). Most sample locations in this study were in the middle or downstream portions of the burn. Based on water flow rates that range from 0.2 to 7.9 mm/s in sloughs in central Water Conservation Area 3A of the Everglades (Harvey et al., 2009), the sites we sampled should have had elevated P concentrations on day 2 or later, equivalent to the day 1 spike,

even under high flow rate conditions. Instead, concentrations dropped rapidly, indicating other factors (i.e., local biotic uptake) reduced P concentrations in water.

Sawgrass stores more TP in belowground parts of the plant that are associated with resource storage than in leaves (Miao & Sklar, 1998). Fire-released pulses of P depend on the concentrations of P in the parts of the plant burned. Prescribed burns in the Everglades are typically conducted with standing water covering the belowground portion of sawgrass and only burn the aboveground portion of sawgrass. Thus, prescribed burns remobilize limited proportions of the total P in sawgrass, and increases in P appear to be short lived due to low P concentrations in sawgrass leaves and

Table 5 Characteristics of fish species caught in minnow traps in at least 80% of 160 plots sampled; mean (±standard deviation)

Variable	Experimental Control	No Nutrients or Light	Light Only	Nutrients Only	Nutrients + Light
G. holbrooki					
Standard length (mm)	23.2 (1.7)	24.0 (1.3)	23.8 (2.2)	24.1 (1.1)	23.8 (1.4)
Mass (g)	0.26 (0.064)	0.28 (0.047)	0.28 (0.053)	0.29 (0.054)	0.28 (0.064)
Condition factor	1.83 (0.23)	1.84 (0.15)	1.98 (0.75)	1.84 (0.16)	1.84 (0.26)
Abundance	28.9 (27.4)	23.0 (11.1)	30.6 (22.8)	34.5 (27.1)	36.5 (23.4)
Relative abundance	56.9 (18.7)	63.0 (17.5)	52.6 (15.3)	62.9 (20.2)	56.5 (15.2)
J. floridae					
Standard length*	27.0 (2.5)	29.3 (2.4)	30.4 (2.9)	27.4 (3.8)	28.2 (2.4)
Mass*	0.61 (0.19)	0.77 (0.19)	0.90 (0.27)	0.63 (0.23)	0.67 (0.18)
Condition factor	2.9 (0.33)	2.9 (0.38)	2.9 (0.42)	2.8 (0.28)	2.8 (0.28)
Abundance*	5.1 (7.8)	4.2 (4.0)	7.3 (6.7)	5.2 (4.9)	11.7 (12.8)
Relative abundance*	7.2 (6.8)	10.0 (8.0)	13.2 (7.2)	11.5 (11.3)	16.4 (11.8)
P. latipinna					
Standard length	25.0 (3.8)	26.5 (6.4)	28.5 (3.9)	24.8 (4.1)	25.4 (3.7)
Mass*	0.43 (0.16)	0.55 (0.33)	0.62 (0.23)	0.44 (0.18)	0.41 (0.18)
Condition factor	2.37 (0.34)	2.39 (0.56)	2.34 (0.31)	2.51 (0.42)	2.29 (0.36)
Abundance	5.7 (5.6)	3.8 (4.5)	6.6 (6.1)	4.3 (4.2)	3.4 (4.9)
Relative abundance	11.8 (11.9)	9.4 (9.1)	11.8 (9.4)	9.7 (10.5)	5.4 (7.3)
H. formosa					
Standard length*	17.8 (1.5)	18.2 (1.3)	17.7 (1.6)	19.4 (1.8)	18.8 (1.9)
Mass	0.13 (0.039)	0.15 (0.050)	0.13 (0.045)	0.16 (0.060)	0.15 (0.051)
Condition factor	2.27 (0.51)	2.43 (0.53)	2.30 (0.67)	2.14 (0.35)	2.11 (0.46)
Abundance	3.7 (3.0)	3.0 (3.0)	4.8 (6.2)	1.8 (2.4)	3.4 (4.2)
Relative abundance*	11.2 (9.3)	8.8 (8.1)	9.5 (9.1)	3.5 (4.2)	5.5 (6.7)

* Letters indicate significant difference of means between treatments grouped by factor (e.g., light vs. no light)

likely rapid uptake by periphyton. TP concentrations in water in this study were much lower than TP concentrations released by fire in cattail (which stores more P) in the Everglades (Miao et al., 2010). Conversely, wildfires often occur in this ecosystem when water levels are below the marsh surface and often burn above- and belowground portions of sawgrass, releasing much more P than prescribed burns. Thus, the P dynamics we documented are not necessarily likely to be transferable to wildfires. In an oligotrophic wetland, any remobilization of nutrients, particularly a limiting nutrient such as P in the Everglades, can result in a boost in primary production.

The increases in periphyton cover and periphyton mass per area (dw) we documented after fire indicate that the release of P and light post-burn was sufficient to result in a significant response of periphyton. Hagerthey et al. (2014) reported increased periphyton

in openings created in enriched and transitional areas through the removal of cattail (*Typha domingensis* Pers.) in the north central Everglades. Thomas et al. (2006) saw no difference in periphyton mat composition or daily gross photosynthesis under a similar range of light conditions as used in this study. However, past studies of nutrient or light effects on periphyton in the Everglades have primarily focused on thick mats of periphyton (e.g., Newman et al., 2004; Gaiser et al., 2005; Thomas et al., 2006). In other aquatic systems, light typically results in increased algal biomass (Mosisch et al., 2001; Mokany et al., 2008). Periphyton in a recently burned area with no established periphyton mat, such as plots in this study, may react differently to changes in light conditions than an established periphyton assemblage in a thick mat.

Periphyton collected in sawgrass ridges in this study generally grew as a thin epipelic layer, which

may be more available to herbivores than when growing within a thick, complex mat structure (Geddes & Trexler, 2003; Chick et al., 2008). Periphyton mats in very oligotrophic areas of the Everglades ($\leq$7 µg/L TP in water) tend to be composed primarily (49–83%) of cyanobacteria (McCormick & O'Dell, 1996). Edible, preferred species such as diatoms grow in pockets created during cyanobacterial growth (Geddes & Trexler, 2003). Nutrient enrichment can alter species composition or structure of the mat and thereby increase edibility of periphyton (Geddes & Trexler, 2003; Chick et al., 2008; Sargeant et al., 2011). While we do not have species composition data to confirm edibility, this information suggests that the increase of periphyton in burned sawgrass stands may have provided an additional food resource for herbivorous species where periphyton was previously limited or non-existent. Further studies determining changes in periphyton species composition and periphyton mat edibility are needed to document changes in food resources for aquatic organisms that fires may facilitate.

Contrary to our prediction, the fish assemblage showed a relatively rapid and pulsed, rather than sustained, response to prescribed fire. The total fish assemblage increased in abundance for approximately 3 weeks (sampling periods 2 and 3) in burn treatments. This increase in fish abundance took approximately 2 weeks to be exhibited, a lagged response that may have been related to the spike in P concentrations in water and increase in periphyton cover and biomass in the burn. While total fish abundance increased temporarily in burn treatments, it did not consistently translate into increases in overall fish size or condition factor. Over the duration of this experiment, fish showed a lot of variability in all metrics with no consistent trend, indicating that burns did not increase overall fish size or condition factor. The throw trap data supported the interpretation of the minnow trap CPUE data as being indicative of patterns of fish density among treatments and through time. This is contrary to the creation of openings in dense, highly enriched areas of cattail in the Everglades where density of small fish did not change (Hagerthey et al., 2014).

Light treatments did not affect the biotic community to the same extent as the combination of light and nutrients. Vegetation height and periphyton cover appear to have responded more to light than nutrients. However, the fish community had a limited response

to the light treatment. Diversity was greater and flagfish were more abundant in light than no-light treatments, but other responses were greater in no-light treatments or either nutrient treatment. This limited response to the light treatment is surprising given that more light and a limited overstory should make fish more vulnerable, especially to avian predators, and thus less abundant. Underwater structure was not purposefully altered in these treatments so the limited response from fish suggests the fish may not have perceived a difference in predation risk despite the removal of the overstory (i.e., sawgrass).

Fish are highly mobile organisms that can respond relatively quickly to changes in the environment (DeAngelis et al., 2010; Hoch et al., 2015), especially at the scale of these experimental plots. Thus, fish may have concentrated in the burn for the first few weeks to exploit new food resources resulting from the burn and then dispersed. This temporary concentration of fish in a burned area may be beneficial to predators such as wading birds. Increased density of prey has been suggested to play a role in attracting wading birds (Gawlik, 2002). However, Venne and Frederick (2013) reported that wading birds prefer burned areas over deeper sloughs in the Everglades for foraging, likely due to increased accessibility (despite decreased density) of prey.

Species respond to environmental changes differently based on availability of preferred food resources (e.g., Reimer, 1970) and predation risk (e.g., Dorn et al., 2006). As expected, individual species of fish responded differently to treatments. Least killifish, the smallest fish species captured, were 1–2 mm longer (6–11% length increase) in burned than unburned areas, a biologically significant size difference for this species. Larger female least killifish produce more broods and more juveniles per brood than smaller females (Leips & Travis, 1999). Thus, the increase of nutrients in burns could increase reproductive output of this species via increasing female size. Conversely, smaller flagfish and sailfin mollies were captured in burned areas. Differences in size for these species, and also for least killifish, may not be due to growth (Travis et al., 1989), but rather related to habitat choice by different size classes.

In conclusion, the fish assemblage showed a pulsed response to prescribed fire associated with a spike in P concentrations in water in the burn and an increase in periphyton cover and biomass in burns. While we did

not quantify the response of the macroinvertebrate community to fire, we expect that the macroinvertebrates may have a similar pulsed response that is species specific. Our results indicated that effects of light and nutrients were contributors to the chain of effects. Fish responded to the coincident increase in light and nutrients, essentially the conditions resulting from a fire. Concentrations of nutrients available for biotic uptake were limited by concentrations in aboveground plant parts and may result in limited trophic level effects such as we saw in this study. Fire is a naturally occurring phenomenon within the Everglades. The effects of prescribed burns and wildfires in this system are important to understand for the incorporation of fire effects into the restoration of this ecosystem. The prescribed fire monitored in this study was intended as a tool for managing vegetation. These results provide an initial understanding of effects of wetland fire on animal and plant communities in a highly oligotrophic wetland, such as the Everglades. This study suggests that when fire is applied to the Everglades vegetation while soil is inundated, the effects of any nutrient cascade are brief, yet the aquatic community responds at different trophic levels [e.g., periphyton (this study), wading birds (Venne & Frederick, 2013)]. However, we caution that the effects of fire are likely to be highly context dependent. Differences in magnitude, duration, and type of response may be found in (a) less oligotrophic and P-limited systems, (b) cases of wetland wildfires that release orders of magnitude more nutrients by burning into organic soils and root zones, and (c) aquatic systems like streams where nutrient dispersal via flow is more rapid.

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