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PRIMARY RESEARCH PAPER

Wildfire induced changes in aquatic invertebrate communities and mercury bioaccumulation in the Okefenokee Swamp

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Abstract Fire is an important natural disturbance in the Okefenokee Swamp. From April–June 2007, wildfire burned 75% of the wetland area. With the existence of extensive pre-fire data sets on community structure and total mercury of invertebrates, the fire presented an opportunity to assess impacts of wildfire on invertebrates. Post-fire collection of samples occurred in September, December, and May, 2007–2009. Sample sites included 13 burned and 8 non-burned (reference) sites. Comparisons of data among pre-fire, post-fire reference, and post-fire burned sites revealed that the major difference between pre-fire communities and post-fire communities was a decrease in the number of water mites. We also found a decrease in mercury concentrations in amphipods, odonates, and crayfish post-fire. The differences between pre-fire and post-fire samples may be confounded by drought conditions during the baseline study. NMDS ordinations and ANOSIM tests suggested that habitat was an important factor; communities in burned cypress differed from reference cypress. Unexpectedly, burned sites had lower mercury concentrations in odonates and crayfish, with variation again being greatest in cypress stands. These findings and others suggest mercury levels do not follow a predictable pattern but can vary with pre-fire concentrations, variation in water levels, and burn intensity. We found that wildfire in the Okefenokee had little impact on invertebrates in prairies and scrub-shrub thickets, but can affect indicator organisms (*Oecetis*, *Ischnura*, and *Sigara*) in cypress stands. Our study suggests that vegetation type and burn intensity may have impacts on the invertebrate communities and mercury concentrations of organisms.

Keywords Community structure · Fire · *Gambusia* · Macroinvertebrate · Wetland

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Introduction

Wildfire is noted as a significant disturbance in many ecosystems; fire can dynamically change ecosystem structure and function. The significance of fire has been well studied in terrestrial systems, but comprehensive studies in aquatic systems are limited. Aquatic systems can be directly and indirectly affected by fire and it may take years to recover (Gresswell, 1999; Minshall, 2003). Studies suggest changes after fire that include a shift in the dominant invertebrate taxa (de Szalay & Resh, 1997; Minshall, 2003), increases in nutrient levels (Scrimgeour et al., 2001; White et al., 2008; Miao et al., 2010), and releases of mercury into the water column (Kelly et al., 2006). Many wetlands in the United States burn regularly (Middleton, 1999); however, little emphasis has been placed on the impacts fire may have on invertebrate community composition and mercury concentrations of aquatic organisms.

Wildfire near streams in Yellowstone National Park caused a shift of the invertebrate community toward dominance by disturbance-adapted organisms with food webs containing a greater number of generalists in streams from burned areas when compared to reference streams (Minshall, 2003). Canadian Shield lakes in recently burned areas had greater total benthic invertebrate biomass and Chironomidae biomass than in reference lakes (Scrimgeour et al., 2001). Multiple studies (Scrimgeour et al., 2001; Kelly et al., 2006) found nutrient releases into the water column associated with fire.

Today, some wetlands are managed with prescribed fire to promote aquatic invertebrate communities and plant species important to waterfowl (de Szalay & Resh, 1997; Davis & Bidwell, 2008). Experimental burn areas supported higher densities of e.g. water boatmen, dytiscid and hydrophilid beetles, midges, and oligochaetes when compared to control sites (de Szalay & Resh, 1997). However, Davis & Bidwell (2008) did not find statistically different abundances of chironomids, oligochaetes, or water boatman from burned sites in their study of wetland management techniques. These studies provide some insight into wetland fires; however, experimental and prescribed burns are usually less intense than wildfires and may have different impacts on aquatic systems (Gresswell, 1999).

Mercury is of particular concern in wetlands because high water temperatures, low dissolved oxygen, and fluctuating water levels found in some wetlands are conducive to the production of methylmercury (Zillioux et al., 1993; Richardson, 1999; Scheuhammer et al., 2007). Sources of mercury deposition in wetlands may be natural or anthropogenic, and are not easily determined (Lindberg et al., 2007). Regardless of source, mercury is of concern in most ecosystems because of its neurotoxic and immunotoxic effects on organisms (Wolfe et al., 1998). Accumulation of 1–10 ppb can cause acute toxicity in some invertebrate developmental stages (Boening, 2000) and mercury in invertebrates can bioaccumulate in higher trophic levels such as fish, alligators, or wetland birds that may feed on invertebrates (Wolfe et al., 1998; Scheuhammer et al., 2007). Many wetland plants are also capable of mercury uptake (Casagrande & Erchull, 1977), and researchers (Sigler et al., 2003; Biswas et al., 2007) have recorded releases of mercury into the atmosphere from forest fires. Zillioux et al. (1993) suggested that disturbed wetlands (e.g., from fluctuating water levels and fire) are capable of producing more methylmercury than undisturbed wetlands. Since mercury is of special concern in wetlands, it is important to understand how disturbance such as fire may affect the cycling of mercury through the food web.

The purpose of this study was to examine the effects of wildfire on invertebrate community composition and the total mercury concentrations of select organisms. We analyzed the invertebrate community composition and total mercury concentrations of amphipods, odonates, crayfish and *Gambusia* (mosquitofish) in burned and reference sites and compared these to pre-fire data sets. We hypothesized that (1) wildfire would shift the community structure of invertebrates toward a community of disturbance-adapted generalists with a decline in other invertebrate taxa not adapted for such disturbances. We predicted that samples from the pre-fire data and the post-fire reference sites would have similar community compositions, but would both differ from the post-fire burned sites. In addition to community differences, we predicted that burned sites might have greater Chironomidae biomass. We also hypothesized that (2) total mercury concentrations would be higher in organisms from the burned sites than reference sites because of fire-induced releases of mercury into the water column.

Methods

Study site

The Okefenokee Swamp is located in southern Georgia and part of northern Florida and is one of the largest wetlands in North America. Most (80%) of the swamp is managed as a National Wilderness

Area. The hydrology of the Okefenokee is dominated by precipitation and evapotranspiration (Rykeil, 1984), and water is highly humic but nutrient poor (Flebbe, 1982). The primary wetland habitat types are scrub-shrub thickets, cypress stands, and sedge prairies (Hamilton, 1982). The swamp is a host to many vertebrates including the American alligator (*Alligator mississippiensis*), birds, and numerous fishes. The aquatic invertebrate community is moderately diverse supporting 103 different taxa, dominated by midges (Chironomidae and Ceratapogonidae) and water mites (Hydrachnida), but fairly homogenous in spite of a mosaic of habitat types and changing seasons (Kratzer & Batzer, 2007).

Mercury contamination in the Okefenokee is a concern, and although the exact source of mercury is unknown it has been attributed to atmospheric fallout (Winger & Lasier, 1997). Mercury occurs at moderately high levels for alligators (average 0.8 ppm in muscle; Jagoe et al., 1998) and invertebrates (0–86 ppm; George & Batzer, 2008). Due to high mercury levels, the Georgia Department of Natural Resources has issued fish consumption advisories for *Amia calva* (bowfin), *Centrarchus macropterus* (flier), and *Esox niger* (chain pickerel).

Fire has been recognized as an important ecological disturbance in the Okefenokee and in part helps structure the plant habitats. It is suggested that prairie formation occurs during extreme fires that burn peat and roots completely, preventing the woody vegetation from re-establishing (Cypert, 1961). Historically, most wildfires of the Okefenokee started during the summer months when thunderstorms and lightning moved through the area. Post-settlement fire suppression has reduced the frequency of fire to once every 20–30 years (Cypert, 1961), with records of large fires (burning more than 50% of the area) occurring every 100 years (Yin, 1993).

From April to June 2007, a complex of wildfires moved through the swamp burning about 75% of the total area and leaving only small non-burned pockets. The fire started north of the swamp on private land and within a few days had begun burning wetlands within the refuge. Since the Okefenokee is managed as a National Wildlife Refuge, the fires were not suppressed except to contain them within the refuge to protect private property and surrounding towns. Although reliable data on burn intensity is unavailable, the fire completely burned many cypress stands, scrub-shrub thickets, and surrounding sedge prairies. In some areas, fire moved quickly across the surface of the peat and vegetation causing little damage. Because most areas previously sampled for invertebrate community composition (Kratzer & Batzer, 2007) and mercury content (George & Batzer, 2008) burned, this fire presented a unique opportunity to assess the impacts of fire on aquatic invertebrates and mercury accumulation.

Areas of interest for our study included burned as well as non-burned reference sites that were in close proximity to burned areas. We chose burned sites with obvious evidence of fire. Our reference sites were located in non-burned pockets in close proximity to burned areas. Much of the Okefenokee is inaccessible except by boat and subsequent challenging travel on foot, therefore most of our sites were located in relatively close proximity to boat trails or canals. However, when we chose these sites, we traveled into the habitat interior to minimize edge effects or the influence of open water habitat. Overall, we selected 21 sites: 13 burned sites and 8 reference sites (Fig. 1). The sites were composed of a mixture of the three dominant vegetative habitats of scrub-shrub thickets (5 burned; 3 reference), cypress stands (5 burned; 3 reference), and sedge prairies (3 burned; 2 reference) and were in the same general areas as those sampled by Kratzer & Batzer (2007) and George & Batzer (2008). Sites were centered in the following sub-regions: Chesser Prairie, Chase Prairie, Billy's Lake, Double Lakes, and Durden Prairie (Fig. 1). At our sites, basic water quality parameters i.e. temperature (11.3–38°C), pH (3.3–6.9), conductivity (28.0–191.4 μS/cm), and dissolved oxygen (0.6–11.6 mg/l) varied temporally, but did not differ between burned and reference sites. Total phosphorous was higher in burned sites (0.51 mg/l) than in reference sites (0.19 mg/l) ($F_{1,54} = 6.0$, $P = 0.017$); however, total nitrogen (1.2–49.8 mg/l) did not vary among sites, habitats, or over time. See Beganyi (2010) for a detailed description of water quality methods and results.

Invertebrate community composition

We collected invertebrate community samples over 2 years (September 2007–August 2009), in August/September, December, and May (see Kratzer & Batzer, 2007 for detailed methods). Water depth was <50 cm at most sites, which resulted in all or most of

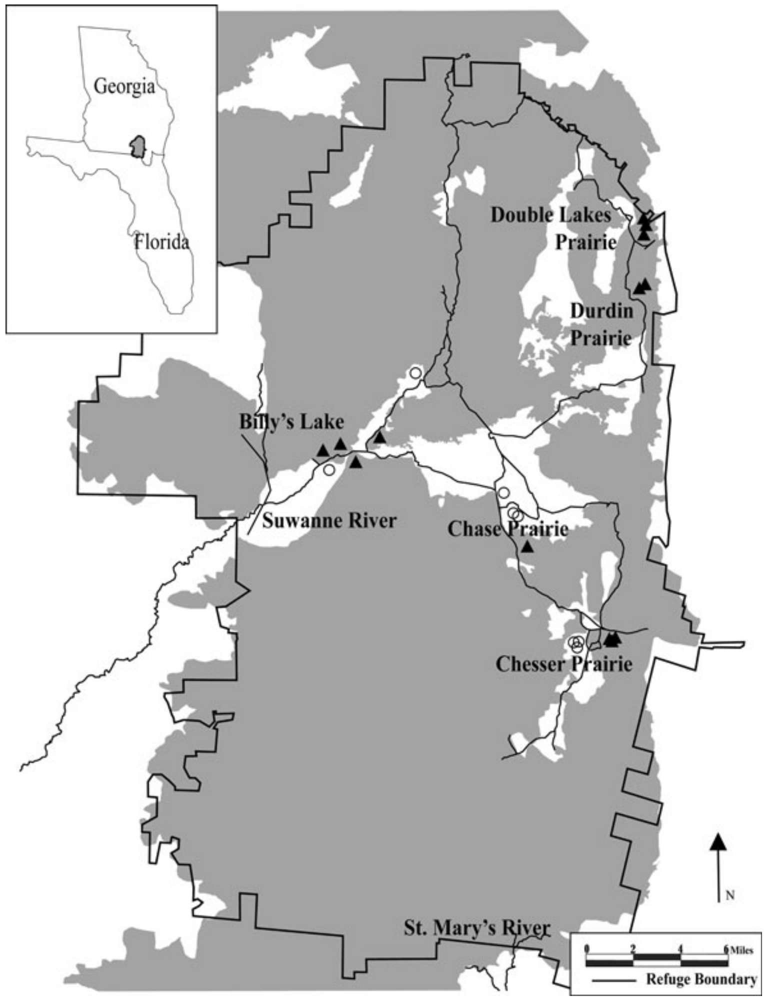

Fig. 1 Map of the Okefenokee showing burned areas (*shaded*) with burned sites (*triangles*) and non-burned areas (*white*) with reference sites (*circles*). Modified map: original courtesy of the USFWS and the Okefenokee NWR

the water column being sampled with the net with each sweep. Among the various sampling devices used in wetlands, sweep nets have been found to capture the greatest richness and are therefore useful in community studies (Turner & Trexler, 1997; Batzer et al., 2001). Samples were stored in 95% ethanol in plastic bags. Fluctuating water levels allowed sampling at most sites on most dates; however, if a site was dry, a sample was not taken (1 site in May 2008, 2 sites in Sep 2008, and 3 sites in Dec 2008).

In the laboratory, community sweep net samples were filtered through a 250 μm sieve, sorted under a dissecting microscope, and organisms were re-preserved in 95% ethanol. Invertebrates were identified to the lowest taxonomic level where possible (usually genus) using standard references (Thorp & Covich, 1991; Epler, 1996; Merritt et al., 2008). The following were identified to family: Ancylidae, Ceratapogonidae, Chironomidae, Cambaridae, Lymnaeidae, and Pyralidae and order: Oligochaeta. Individuals from the family Chironomidae were measured to the nearest millimeter and published length-mass relationships were used to estimate biomass (Benke et al., 1999).

Total mercury content of selected organisms

We repeated sampling protocols from the previous study (for details see George & Batzer, 2008) to collect odonates (dragonfly nymphs, Libellulidae and Corduliidae), crayfish (Cambaridae), and amphipods (scuds, *Crangonyx*), with additional protocols for collecting mosquitofish (*Gambusia*). Mosquitofish were collected and euthanized with MS222 buffered with calcium carbonate in accordance with the UGA

Animal Care and Use Compliance. Samples were stored on ice, and then frozen until analysis. Amphipods, odonates and crayfish were collected from December 2007–December 2008. Beginning in May 2009 we sampled mosquitofish and continued to collect odonates and crayfish until August 2009. We chose to sample mosquitofish because they were ubiquitous throughout the sampling sites, and are commonly used to biologically assess mercury in wetlands (e.g., Liu et al., 2008).

The University of Georgia Agricultural and Environmental Services Laboratory analyzed samples for total mercury using USEPA Method 3052 (1996) for digestion and USEPA Method 245.6 (1991) for the determination of mercury in tissues by cold vapor atomic absorption spectrometry (CVAAS) with detection limits of 0.008 ppb wet weight. The lab follows a stringent quality control protocol and calibrates instruments every 20 samples using certified reference materials. According to Horvat (1996), CVAAS is one of the leading and most reliable methods for mercury determination available.

Statistical analyses

To determine patterns in community structure, we eliminated rare taxa (present $< 10\%$ of samples), then log $(x + 1)$ transformed and analyzed the data using a non-metric multidimensional scaling approach (NMDS; PC-ORD 5). We used a Bray-Curtis similarity distance measure on the slow-and-thorough autopilot option. The slow-and-thorough option uses 250 real and randomized runs, and determines the best solution, and the best dimensionality based on a Monte Carlo test of significance. NMDS ordinations are useful to view community structures and possible groupings among factors; however, these analyses do not include formal testing of significant differences among groups (Clarke & Warwick, 1994). Therefore, an Analysis of Similarity (ANOSIM; Primer 6) was used to verify significant factors. To determine what taxa were driving differences in community structures, an indicator species analysis followed by a Monte Carlo test of significance (5,000 permutations; PC-ORD 5) was used. Indicator values combine information on the abundance of the species within each group and the faithfulness (always present in the group and exclusive to that group) of occurrence (McCune & Grace, 2002). We log $(x + 1)$ transformed Chironomidae biomass values and used a multi-way ANOVA (Proc GLM; SAS 9.2) to assess differences in biomass among burn category, habitat, and date. We also log $(x + 1)$ transformed total invertebrate abundance and used a multi-way ANOVA (Proc GLM; SAS 9.2) to assess differences in abundance among burn category, habitat, and date.

Non-parametric Kruskal–Wallis tests (SAS 9.2) were used to assess differences in total mercury concentrations by organism type, among the burn categories, and habitats. The Kruskal–Wallis test is a ranked test that is useful for non-normal data (Dowdy et al., 2004). When results were significant, Wilcoxon two-sample tests were used for multiple comparisons; we used a Bonferroni corrected global alpha when multiple tests were run in series. Multi-way ANOVAs (Proc GLM; SAS 9.2) were used to determine if any of the water chemistry measures differed among burn category, habitat, and date.

Results

Pre- and post-fire community composition

A total of 31,864 individuals were collected in 109 samples post-fire. Eighty two taxa were identified from 15 orders, 39 families, and 72 genera. The most common families included: Chironomidae 74%, Ceratopogonidae 7%, Crangoncytidae 5%, Hydroptilidae 3%, and Dytiscidae 2%.

NMDS community analysis of pre-fire, post-fire reference, and post-fire burned sites suggested a three-dimensional solution with moderately high stress (18.7) that explained 76% of the variability. There were 112 iterations in the final solution. NMDS ordinations illustrated slight groupings of community structures among the three burn categories confirmed by a one-way ANOSIM (Fig. 2; overall $P < 0.001$). Pre-fire communities and post-fire burned communities differed most (ANOSIM; $P = 0.0001$), and post-fire reference and post-fire burned sites were marginally different (ANOSIM; $P = 0.063$), while pre-fire and post-fire reference communities were similar (ANOSIM; $P = 0.092$). Pre-fire communities were dominated by water mites and midges; while water mites contributed little (<1% of total invertebrate abundance) in the post-fire studies.

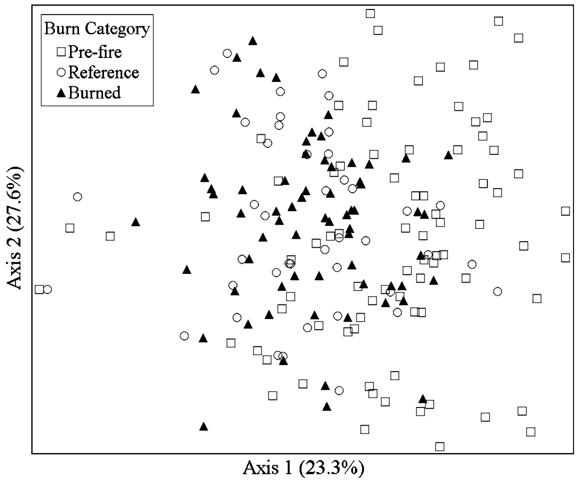

Fig. 2 NMDS ordination of pre-fire, post-fire burned, and post-fire reference sites (for all habitats combined) showing slight groupings among burn categories. The plot is comprised of Axis 1 ($r^2 = 0.233$), Axis 2 ($r^2 = 0.276$), and Axis 3 (not shown, $r^2 = 0.252$) that explained 76% of the variability; overall stress for NMDS analysis = 18.7. One-way ANOSIM suggested that the groupings were significantly different between pre-fire and post-fire burned sites ($P = 0.0001$), but not for the other burn category combinations

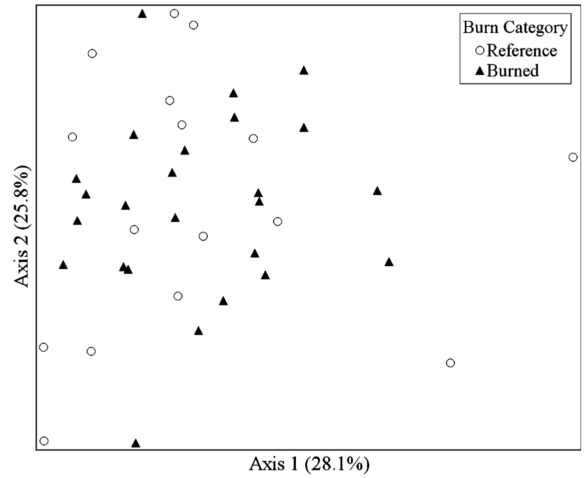

Fig. 3 NMDS ordination of cypress only habitat sites showing groupings of burned and reference sites. Plot comprised of Axis 1 ($r^2 = 0.281$), Axis 2 ($r^2 = 0.258$), and Axis 3 (not shown, $r^2 = 0.243$) that explained 78% of the variability; overall stress for NMDS analysis = 16.4. One-way ANOSIM suggested that the groupings were significantly different ($P = 0.025$)

Post-fire community composition: burned and reference sites

NMDS analysis of post-fire burned and post-fire reference sites (all habitats combined) suggested a three-dimensional solution with moderately high stress (18.4) that explained 75% of the variability. However, NMDS ordinations did not illustrate clear groupings of community structures between burned and reference sites (for all habitats combined), and a one-way ANOSIM contrasting burned and reference sites was marginally non-significant ($P = 0.066$).

To determine if the effect of burn category was modified by other spatial (habitat) or temporal (sample date) factors, we conducted two-way crossed ANOSIMs with burn category and either sample date or habitat as the second factor. When we examined differences between burn categories across habitats (in a two-way crossed ANOSIM), we found significant differences ($P = 0.049$); similarly, when we examined habitats across burn categories, the differences were also significant ($P = 0.001$). We did not find significant differences when we examined differences between burn categories across time nor when we examined time across burn categories.

In prairie and scrub-shrub habitats, the community structure of burned and reference sites did not significantly differ. However, in cypress habitats, burned and reference sites were different ($P = 0.025$). NMDS ordination of the community structure in cypress sites illustrates the separation between burned sites and reference sites (Fig. 3). Indicator analysis suggested that *Ischnura* (Coenagrionidae; $P = 0.046$) and *Oecetis* (Leptoceridae; $P = 0.039$) were indicators of reference sites, and *Sigara* (Corixidae; $P = 0.039$) was an indicator of burned sites.

A multi-way ANOVA of total macroinvertebrate abundance did not reveal differences among burn category, habitat, date, or interactions between factors (overall $P = 0.07$). A multi-way ANOVA of Chironomidae biomass did not reveal differences among burn status, habitat, date, nor interactions between factors (overall $P = 0.469$).

Pre- and post-fire comparison of mercury

Total mercury concentrations in invertebrates (amphipods, odonates, and crayfish) from the 1998–2000 study were considerably higher than the concentrations found in the post-fire study. All organisms had lower total mercury concentrations in 2007–2009 (0–0.55 ppm) than years before the fire 1998–2000

(0–86 ppm). Wilcoxon two-sample tests indicated that pre-fire values were significantly higher than post-fire values for all organisms (amphipods: $H = 57.2$, df = 1, $P < 0.001$; odonates: $H = 52.9$, df = 1, $P < 0.001$; crayfish: $H = 23.7$, df = 1, $P < 0.001$).

Post-fire comparison of mercury: burned and reference sites

Kruskal–Wallis tests indicated that concentrations in odonates and crayfish were significantly lower in burned than reference sites (odonates: $H = 7.2$, df = 1, $P = 0.007$; crayfish: $H = 4.2$, df = 1, $P = 0.040$), while concentrations in amphipods and mosquitofish did not differ between burned and reference sites (Fig. 4). Kruskal–Wallis test with multiple comparisons revealed that crayfish and odonates did not differ in total mercury, but were lower than levels from amphipods and mosquitofish, which also did not differ from each other (reference sites: $H = 25.4$, df = 3, overall $P < 0.001$; burned sites: $H = 47.3$, df = 3, overall $P < 0.001$).

Conducting separate comparisons for individual habitat types for each organism only revealed that mercury in odonates from burned cypress habitats was lower than in reference cypress habitats ($H = 9.6$, df = 1, $P = 0.002$). All other organism and habitat combinations were not significant. In some cases (e.g., crayfish), differences between overall and habitat specific results may have been related to small sample sizes.

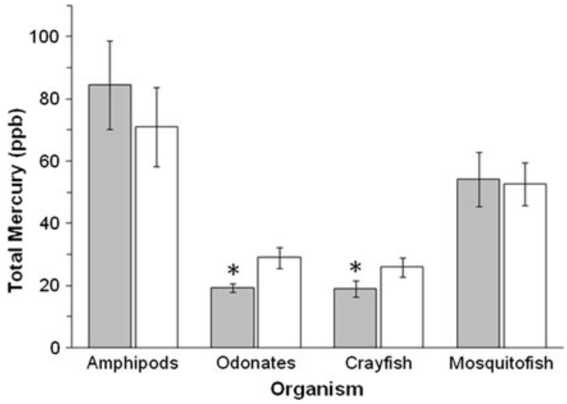

Fig. 4 Total mercury concentrations of amphipods ($n = 67$ samples), odonates ($n = 73$ samples), crayfish ($n = 60$ samples), and *Gambusia* ($n = 25$ samples) of the Okefenokee Swamp. Open bars are means from reference sites and shaded bars are means from burned sites; error bars represent ±1 SE. Wilcoxon two-sample tests suggest that concentrations in odonates and crayfish were lower in burned sites than reference sites (odonates: $H = 7.2$, df = 1, $P = 0.007$; crayfish: $H = 4.2$, df = 1, $P = 0.040$). *Asterisks* show a significant difference from reference organism concentrations

Discussion

Invertebrate community response to wildfire

We hypothesized that wildfire would shift the invertebrate community composition toward a community of disturbance-adapted generalists. We predicted that pre-fire data samples and post-fire reference sites should have similar community compositions, but both would differ from the post-fire burned sites. While the data suggested community differences among the three burn categories (pre-fire, post-fire burned, and post-fire reference), factors other than fire may be responsible for variation between pre- and post-fire periods such as natural temporal changes in the Okefenokee Swamp (e.g. variation in water levels). For example, Kratzer & Batzer (2007) found that the Okefenokee invertebrate community was dominated by midges and water mites. After the fire, midges still dominated; however, water mites were not among the most common taxa. These differences could be confounded by the presence of drought conditions during the baseline study where water levels were much lower than the post-fire study and may not reflect impacts of fire. Therefore, most of our discussion focuses on the post-fire differences between reference and burned sites.

There were only marginal, albeit insignificant differences in overall community composition between burned and reference sites and NMDS analyses did not illustrate clear groupings. However, when habitats were examined individually, we found that invertebrates in cypress habitats were most affected by fire. Most differences in cypress sites could be attributed to three indicator organisms: *Sigara* was associated with burned sites; and *Oecetis* and *Ischnura* were associated with reference sites. This suggests that *Sigara* may be adapted to fire, while *Oecetis* and *Ischnura* may be negatively affected by fire. Overall, most invertebrate taxa in the Okefenokee seem unaffected by fire. Since water levels were relatively stable, taxa may have had adequate refuge during the fire and may only be affected by indirect effects of fire (such as nutrient releases and algal blooms). Wetland invertebrates are adapted to dealing with many stresses therefore they may show little response to fire compared to stream (Minshall, 2003) and lake (Scrimgeour et al., 2001; Kelly et al., 2006) communities.

Similar to our findings, a study of prescribed burn in a California marsh found a greater density of corixids in burned areas than reference areas (de Szalay & Resh, 1997). In bioassessment, corixids have frequently been found dominating anthropogenically impacted wetlands (Helgen & Gernes, 2001; Hartzell et al., 2007). We observed dense algal blooms in our burned sites that corresponded to increased phosphorous levels, *Sigara* corixids may have benefitted from these changes because they are generalist herbivore feeders (Merritt et al., 2008).

Trichoptera (caddisflies) are commonly used as indicators of stream quality, and although not found in large numbers in wetlands, they can also be useful in determining wetland condition (Burton et al., 1999; Helgen & Gernes, 2001; Wilcox et al., 2002; Hartzell et al., 2007). Although richness of Trichoptera did not vary between burned and reference sites (3 taxa found in both), we found that the genus *Oecetis* was more prominent in reference cypress habitats when compared to burned cypress habitats. *Oecetis* is considered a moderately intolerant taxon and it tends to be absent in human disturbed wetlands (Helgen & Gernes, 2001). Odonata (dragonflies and damselflies) are another taxonomic group commonly used as indicators of human disturbance in wetlands (Burton et al., 1999; Helgen & Gernes, 2001; Wilcox et al., 2002; Hartzell et al., 2007). In the Okefenokee, Porter et al. (1999) suggested that odonates might be especially useful bioindicators because of the diverse nature of the fauna. Our study suggested that the damselfly, *Ischnura* (Coenagrionidae) and caddisfly, *Oecetis* are both sensitive to fire. Although we found these differences between burned and reference sites, differences among three taxa are a relatively small change on a community scale and therefore do not strongly support our hypothesis that the community would be dominated by disturbance-adapted organisms.

We were surprised to find that fire did not affect biomass of Chironomidae as it had in other studies (de Szalay & Resh, 1997; Scrimgeour et al., 2001). However, these studies used different sampling techniques (benthic corer, Eckman-Birge grab). D-nets sample midges living epiphytically more efficiently than those living in the sediment (Henke, 2005), so we may have underestimated responses of benthic midges in our study. Alternatively, prescribed burns in managed wetlands (e.g., de Szalay & Resh, 1997) are typically conducted when habitats are dry, and thus sediments themselves are directly affected.

Our study suggests that invertebrate communities in cypress stands of the Okefenokee were more impacted by fire than those in sedge prairies or scrub-shrub thickets. Based on personal observations, burn intensity seemed to be greater in cypress stands and the sites we chose were completely burned (with little canopy left intact). In these areas, we frequently observed algal blooms. Increased algal growth in these areas could be attributed to increased phosphorous levels (in burned areas) and an open canopy. Future studies of wildfire in wetlands should take habitat conditions and burn intensity into consideration to determine the exact impacts on aquatic invertebrates.

Total mercury of selected organisms after wildfire

We hypothesized that fire would increase total mercury levels in aquatic organisms. However, our study found lower rather than higher total mercury concentrations post-fire, albeit only in selected organisms. When comparing our results with those collected several years before the fire (George & Batzer, 2008), mercury levels declined in all taxa sampled including a 91% decline in amphipods, and 67% in odonates and crayfish. This post-fire decline occurred in both burned and non-burned areas, suggesting either that fire had a pervasive effect, even beyond the areas burned directly, or that the decline was caused by factors other than fire (e.g., fluctuating water levels, temporal variation in sediment mercury levels, methylation rates, or rates of mercury input; variation between the analytical laboratories providing data). George & Batzer (2008) suggested that high mercury levels (in permanently flooded sites) in May 2000 could have resulted from drought conditions. Since the high levels in the pre-fire study may be associated with drought or other factors besides fire, we focus our discussion on post-fire burned and reference sites.

When comparing burn and reference sites from the same time period, odonates and crayfish both had lower levels of total mercury in burned sites than reference sites overall. When focusing on individual habitats, we only found that total mercury levels in odonates living in burned cypress areas were lower than those living in non-burned cypress. This indicates that impacts on total mercury were greatest in burned cypress, as was the case with invertebrate community responses. Analyzing total mercury in individual habitats reduced sample size and may have obscured some trends in other organisms or habitats. However, increased burn intensity (i.e. from greater fuel stores) in forested habitat versus shrub or herbaceous vegetation seems a likely reason for pronounced responses in cypress.

Kelly et al. (2006) found that after the catchment for Moab Lake (Canadian Rocky Mountains) partially burned, methylmercury in fishes increased fivefold post-fire when compared to reference lakes. They attributed the differences to a shift in the fish diets and increased mercury inputs, i.e., increases in lake productivity caused food chains to be longer, which affected the structure of aquatic communities and concentrations of mercury (Kelly et al., 2006). In contrast, mosquitofish in the Okefenokee did not differ among burn categories, but these fish occupy a fairly low position in the food chain. It is possible that larger, piscivorous fish in the Okefenokee had higher mercury levels after the fire and future studies may benefit from including larger fishes in analyses.

Similar to our results, Allen et al. (2005) found that levels of methylmercury decreased in *Gammarus lacustris* amphipods and *Cordulia shurtleffi* odonates in Canadian lakes after a major fire, but was attributed to differences in the diets of these organisms between the two treatment times. Pickhardt et al. (2002) demonstrated that algal blooms can reduce methylmercury concentrations in zooplankton via biodilution. As mentioned, we found higher levels of total phosphorous and observed algal blooms in burned sites (mostly cypress and some scrub-shrub sites). Perhaps these algal blooms caused biodilution of mercury in burned areas of the Okefenokee, and levels of mercury in some invertebrates thus declined. Another study by Garcia & Carnignan (1999) failed to find differences in methylmercury levels in zooplankton from burned and reference lakes after the catchments partially burned. They attributed this to changes in soil mercury speciation, loss of mercury through volatilization, and nutrient pulses following fire that diluted mercury levels available to biota.

Horvat (1996) describes how many factors can affect mercury levels in organisms (e.g. diet and age of organism, physical attributes of the surrounding system), and suggests that mercury cycling will not be similar in all aquatic systems or aquatic organisms. Others have suggested that variation in burn intensity and total area burned could also affect mercury cycling in aquatic systems (Allen et al., 2005). Since mercury cycling depends on many factors and studies provide conflicting conclusions it seems likely that post-fire changes in mercury cycling in aquatic systems will be difficult to predict.

Implications

To our knowledge, our study is the first examining the effects of natural wildfire on invertebrate communities and total mercury concentrations of organisms in a wetland. In the Okefenokee, fire impacts on both invertebrate community structure and mercury levels were particularly pronounced in cypress habitats. Presently, a long term study is focusing on cypress habitats and the three indicator organisms.

Prescribed fire is often used in wetlands to increase favorable habitat and invertebrate food sources for waterfowl. However, our study in the Okefenokee found that invertebrates were somewhat impervious to the effects of fire. It will be difficult to predict post-fire mercury concentrations in organisms because studies produce contradictory results. Effects of wildfire will be especially difficult to predict because their timing, duration, and intensity are so variable. All of these factors will complicate management of large natural wetlands like the Okefenokee.

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