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Altered Swimming Performance of a Benthic Fish (*Erimyzon sucetta*) Exposed to Contaminated Sediments

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Abstract. Numerous field surveys suggest that coal combustion wastes (ash) adversely affect fish populations, but few controlled laboratory studies have evaluated the responses of individual fish to ash exposure. Available information suggests that sublethal effects of ash, including decreased growth rates and reduced fecundity, may be important manifestations of ash toxicity. Here, we hypothesized that ash may also alter swimming performance, which could ultimately have important implications for the autecology of affected species. To test this hypothesis, we measured sprint speed and critical swimming speed (U_{crit}) of juvenile lake chubsuckers (*Erimyzon sucetta*) exposed to ash in the laboratory. Fish exposed to ash for 90–100 days accumulated significant concentrations of As, Se, Sr, and V; exhibited severe fin erosion; and had reduced sprint speed and U_{crit}. Compared to controls, sprint speed of ash-exposed fish was reduced by 30% at 5 cm and the percent reduction was further reduced to 104% at 20 cm. Critical swimming speed was approximately 50% lower in fish exposed to ash compared to controls. Additionally, the typical positive relationship between standard length and U_{crit} was absent in fish exposed to ash. Because reductions in swimming performance could not be attributed to pollutant-induced differences in body condition or fin morphology, we hypothesize that physiological disruptions (*e.g.*, increased energy demands, decreased oxygen uptake or transport) are responsible for the observed effects and warrant further attention.

Release of effluent from coal-burning power plants has frequently been linked to fish population declines and changes in aquatic community structure, but few controlled laboratory studies have examined the mechanisms underlying such alterations. Most field surveys at sites polluted by power plant effluent attribute causation of population- and community-level changes to exposure to Se, a potent teratogen associated with coal combustion waste (hereafter referred to as ash) (Garrett and Inman 1984; Sorensen 1988; Lemly 1993, 1998). In support of this contention, studies on fish from ash-impacted sites have documented maternal transfer of high quantities of Se and concomitant increased frequency of developmental abnormalities in offspring (Gillespie and Baumann 1986; Lemly 1998). Although reproductive anomalies associated with excessive Se exposure may play a central role in declining fish populations within ash-impacted habitats, other more subtle effects of ash may also contribute to observed alterations in community dynamics. For example, recent studies indicate that lake chubsuckers (*Erimyzon sucetta*) exposed to ash accumulate Se, as well as other trace elements, resulting in reduced growth rates and severe fin erosion (Hopkins *et al.* 2000a, 2002). If such alterations are common among fish exposed to ash, the viability of exposed fish populations may be compromised.

The purpose of the current study was to determine whether swimming performance of fish (*E. sucetta*) was altered following experimental exposure to ash. Because swimming performance is central to many aspects of fish biology, reduced performance following exposure to ash could have important implications for inter- and intraspecific interactions, perhaps ultimately reducing fitness in affected individuals. We quantified two performance parameters, sprint speed and critical swimming speed (U_{crit}) relating to burst and prolonged swimming, respectively. We chose to examine burst and prolonged activities because of their importance to different aspects of fish biology. Burst locomotion is important for such activities as feeding, predator avoidance, and competitive interactions (Huey 1980; Reidy *et al.* 2000). In contrast, sustained or prolonged swimming activities may be critical for seasonal behaviors relating to migration and reproduction (*e.g.*, courtship and nesting).

Materials and Methods

Experimental Design

Lake chubsuckers (approximate standard length 40 mm) were collected from an historically unpolluted Carolina Bay (Bay 100 on the Savannah River Site) using minnow traps in June 2000. After transport

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to the laboratory, fish were allowed to acclimate to laboratory conditions for approximately 4 weeks. During the acclimation period, fish were held in 72-L tanks containing artificial softwater (US EPA 1991) at 25°C and were fed ground Tetramin fish flakes *ad libitum*.

On 13 July 2000 fish were randomly assigned to individual 38-L experimental tanks containing either weathered coal ash–contaminated sediments (ash) collected from the receiving ditch at the D-Area coal-burning power plant on the SRS (for site description, see Hopkins *et al.* 2000b) or sand (control) collected from the upper reach of Upper Three Runs, a stream with no history of ash input (n = 12 fish per treatment). The bottom of each tank was covered with approximately 1 cm of substrate, and all tanks were equipped with carbon filters, heaters (which maintained tank temperatures near 25°C; $\bar{x} \pm$ SE: control = 25.67 ± 0.08°C, ash = 25.74 ± 0.09°C), and aeration. Each tank also contained a 10 × 10 × 2-cm clay refuge, which had no bottom so that fish using them maintained exposure to sediments. Tanks were arranged in four randomized blocks on laboratory shelves (three replicates of each sediment type per block).

Prior to tank assignment, we measured mass (nearest 1.0 mg) and standard length (nearest 0.01 mm) of each fish. Standard length was determined by taking a dorsal image of each fish using Morphosys® visual imaging analysis software according to methods described by Heulett *et al.* (1995). The procedure was repeated three times, and the mean of the measurements was used for that fish. On initiation of the study, mean standard length and mass of fish were similar between treatments ($\bar{x} \pm$ SE: ash: 46.07 ± 1.23 mm and 1.936 ± 0.13 g; control: 46.24 ± 1.14 mm and 1.945 ± 0.13 g).

Fish were fed 125 mg of ground Tetramin fish food three times per week (equivalent to 19.3% of their initial body mass/week) for the first 3 weeks of the study. To accommodate fish growth, food rations were increased by an additional 75 mg/week at 3–4-week intervals for the remainder of the study. Because *E. sucetta* graze ground fish food from surface sediments, they ingest sediments while feeding. Tanks were inspected 4–5 days per week to document fish survival and to monitor food consumption. Water chemistry (dissolved oxygen, pH, conductivity) was monitored weekly; dissolved oxygen and pH remained similar between treatments ($\bar{x} \pm$ SE; DO: control = 7.61 ± 0.03 mg/L, ash = 7.59 ± 0.02 mg/L; pH: control = 7.05 ± 0.04, ash = 7.20 ± 0.02) whereas conductivity was higher in the ash treatment ($\bar{x} \pm$ SE; control = 198.98 ± 3.14, ash = 223.89 ± 3.11).

Swimming Performance

After 78 days of exposure in experimental tanks, we measured sprint speeds of each fish. We define sprint speed as the distance swum (5, 10, and 20 cm) divided by the time required to swim the respective distance when starting from a motionless position (expressed as cm/s). Before conducting the sprint speed trials, each fish was placed in a perforated 600-ml holding vessel suspended within each individual's aquarium for 15–20 h. The vessels enabled each fish to remain within its respective tank without having access to food or sediment. The following day, sprint speeds were determined by placing each fish in a 5-m plastic swim track, similar to that used by Hopkins *et al.* (2000b). The track was 4 cm wide, thus encouraging fish to swim unidirectionally and limiting the influence of side-to-side motion on our sprint speed estimates. Once a fish remained motionless in the track, they received a single prod with a blunt stainless steel probe on the right side of the caudal peduncle. The procedure was repeated 10–12 times per individual, over a 10–30-min time interval (depending on how quickly each fish would voluntarily become motionless between prods). Sprints occurred over a background marked at 1.0-cm increments and were recorded using a video camera. Following the sprint trial, each fish was weighed and ash-exposed fish were qualitatively ranked in relation to each other (from 1 [lowest] to 11 [highest]) based on severity of caudal fin erosion. Three observers ranked caudal fin erosion independently and were in 100% agreement on fish fin erosion ranks. Fish were returned to their respective experimental tanks following sprint speed trials. Sprint speeds were later calculated using a frame-by-frame advance on a VCR with accuracy to 0.03 s (Raimondo *et al.* 1998; Hopkins *et al.* 2000b). The time it took for each individual to swim 5-, 10-, and 20-cm distances was calculated for each sprint. The fastest sprint speed for each individual at each distance was used for statistical comparisons.

Fish were allowed to recover from sprint speed trials in their experimental tanks for 12 days before U_{crit} trials were initiated. Critical swimming speeds were determined using a laminar-flow swim tunnel similar to the design of Vogel and LaBarbera (1978). Water was continuously propelled through the swim tunnel using a 0.75-hp DC motor (Dayton, model #2Z846D) with a 6-cm propeller connected to a Dayton 0.75-hp DC speed control device. Laminar flow in the swim tunnel was achieved using a Plexiglas collimeter preceding the propeller and two soda straw arrays upstream from the swim area (Vogel and LaBarbera 1978). Because visual dye comparisons of laminar flow revealed that water velocity is slightly reduced along the straight sides of the tunnel compared to the center of the tunnel, a cylindrical swim chamber was suspended in the center of the tunnel to limit the swimming area available to fish. The 17-cm-long swim chamber was constructed of clear 7-cm-diameter PVC pipe and was suspended in the center of the swim tunnel by two wire mounts. For every U_{crit} trial, the motor speed controller was calibrated against water flow velocity by placing a Marsh-McBirney 201D flow meter (Marsh-McBirney, Frederick, MD) 0.25 cm behind the swim chamber. The entire swim tunnel was covered with fine mesh to prevent visual disturbances and all swim trials were conducted under dim ambient light. Continual aeration was provided by an airstone submerged downstream from the swimming area. Mean (± SE) water temperature during the swim trials was 25.61 ± 0.08°C.

Each fish was removed from its holding vessel and placed in the swim tunnel at a water velocity of 2 cm/s. After 30 min, water velocity was increased to 5 cm/s. At these two low water velocities, fish sometimes attempted to rest against the back support screen; this behavior was discouraged by gently prodding fish with an aluminum probe. Critical swimming speed was determined by increasing water velocity in 5 cm/s increments every 30 min (Farlinger and Beamish 1977; Nelson 1989). At higher water velocities, fish initiated burst-and-coast swimming (Webb 1998) before ultimately becoming exhausted. The U_{crit} trial was terminated when the fish rested on the downstream support screen and repeated prods could not stimulate the fish to resume swimming. Critical swimming speed was calculated according to the formula described by Brett (1964):

$$U_{\text{crit}} = V_f + [(T/t)*dV], \tag{1}$$

where U_{crit} = critical swimming speed (cm/s), V_f = highest velocity maintained for 30 min, T = time of complete exhaustion at final velocity, t = interval duration (30 min), and dV = velocity increment (5 cm/s). Critical swimming speeds were determined for one or two fish per day over a 10-day period (n = 9 per treatment). At the end of each trial, fish were measured with Morphosys and weighed before being frozen for future lipid and trace element analysis.

Lipid and Trace Element Analyses

Whole fish and sediment samples from the ash and control tanks were lyophilized and homogenized prior to analysis. A subsample of each homogenized fish was used for determination of nonpolar lipid content by petroleum ether extraction (for methods see Hopkins *et al.* 2000a, 2002). Sediment and the remaining fish homogenate were digested and analyzed for trace element concentrations (As, Cd, Cu, Se, Sr, and V) according to the following procedures. Approximately 200 or 350 mg of dry sample (fish and sediment, respectively) was used for digestion. Nitric acid (2.5 or 5.0 ml, fish and sediment, respectively) was added to samples before digestion in a microwave (CEM, Matthews, NC) with heating steps of 60%, 60%, 70%, and 80% microwave power for 10, 10, 15, and 20 min, respectively. Next, 1.0 ml H_2O_2 was added to the samples and microwaved at the same power and duration as the HNO_3 digestion. After digestion, samples were brought to a final volume of 10 or 25 ml (fish and sediment, respectively) with double-distilled water. Water samples from ash and control tanks were prepared by filtering (0.45 μm filter) 20 ml water from the experimental tanks ($n = 8$/treatment) before acidifying the sample with 1.4 ml nitric acid. Trace element analysis was performed by ICP-MS (Perkin Elmer, Norwalk, CT) on samples diluted 1:1 with double-distilled water. Calibration standards covering a range of 1–500 μg/L were prepared daily by serial dilution of NIST traceable primary standards. Certified reference material (Tort 2 and Mess 2; NRC, Ottawa, Canada) and blanks were included in the digestion and analysis procedure for quality control purposes. Mean percent recoveries for trace elements in certified reference material ranged from 103.7% to 119.3%. Mean variability in percent recoveries of certified reference materials between digestion sets ranged from 2.7% to 10.4%.

Statistical Analyses

Because trace element concentrations in sediment and water samples were often below detection in the control treatment and sometimes in the ash treatment, we did not conduct formal statistical analyses of these data. Trace element concentrations in fish from the experimental treatments were compared using MANOVA with sediment type as the main effect in the model. Pillai's trace statistic was used to test the null hypothesis of no treatment effect.

Fish growth was not compared statistically because fish were sacrificed asynchronously over the last 10 days of the study. The presence of fin erosion was compared between ash and control fish using a Fisher's exact test. Condition factor ($K =$ [fish mass (g)/fish standard length^3 (cm)] * 100; Anderson and Gutreuter 1984) of fish at the end of the study was compared between sediment treatments using a *t*-test with a correction for heterogeneity of variance. Percent nonpolar lipid content of fish was compared between sediment treatments using ANOVA on untransformed data.

We used repeated-measures ANOVA to test for effects of sediment and sprint distance on sprint speed. Preliminary analysis of sprint data indicated no significant effects of mass or standard length (or their interaction with treatment) on sprint speed at any of the sprint distances (ANCOVA; $p > 0.162$ in all cases). Sprint speed was log-transformed prior to analysis to meet assumptions of ANOVA. We tested for relationships between condition factor, nonpolar lipid concentrations, and sprint speed at each distance using Spearman rank order correlation coefficients. We also used Spearman rank order correlation coefficients to test for a relationship between caudal fin erosion ranks and ranked U_{crit} values among fish exposed to ash; only ash-exposed fish exhibited caudal fin erosion.

We used ANCOVA to test for effects of sediment treatment on U_{crit} values with standard length included as a covariate. Data used in this analysis did not require transformation to meet assumptions of normality and homogeneity of variance. Within each sediment treatment, linear regression was used to test for relationships between standard length and U_{crit} as well as between mass and U_{crit}. For all fish we tested for relationships between condition factor, nonpolar lipid content, and U_{crit} using Spearman rank order correlation coefficients. We also used Spearman rank order correlation coefficients to test for a relationship between caudal fin erosion ranks and U_{crit} among fish exposed to ash.

Results

In general, trace element concentrations were elevated in water and sediments from ash tanks compared to controls (Table 1) and were within the range of concentrations documented at the contaminated field site over the last 25 years (Rowe *et al.* 2002). With the exception of Cu, dissolved concentrations of all measured elements were higher in water from ash tanks than in control tanks. In several cases, water concentrations were more than an order of magnitude higher in ash tanks compared to controls. Similarly, sediment concentrations were much higher in ash than in sand from control tanks. Fish exposed to ash for 90–100 days accumulated significant whole body concentrations of trace elements (Pillai's trace = 0.889, $F_{6,15} = 21.29$, $p < 0.001$; Table 1). Specifically, concentrations of As, Se, Sr, and V were two to eight times higher in ash-exposed fish than in controls. Whole-body concentrations of Cd and Cu were similar in fish from both treatments.

Survival was high and similar among fish in both groups; two ash fish and one control fish died during the study. Control fish were larger than ash fish at termination of the study ($\bar{x} \pm$ SE; control: 57.96 ± 1.00 mm and 4.013 ± 0.19 g; ash: 55.67 ± 1.23 mm and 3.446 ± 0.25 g). Mean condition factor of fish did not differ between treatments (*t*-test, correction for unequal variance; $p = 0.302$). Percent nonpolar lipids in fish did not differ between sediment treatments ($\bar{x} \pm$ SE; control: 7.09 ± 0.68; ash: 6.75 ± 0.48; $p = 0.71$). The presence of caudal fin erosion differed significantly between treatments ($p < 0.001$); 80% of surviving fish exposed to ash exhibited caudal fin erosion and 70% exhibited pectoral fin erosion, whereas no fin erosion occurred among control fish.

Sprint speed was influenced by sediment type, but this influence was also dependent on sprint distance (*i.e.*, there was a significant interaction between sediment and distance; Table 2). At all sprint distances, fish exposed to ash were slower, but the reductions in sprint velocity became more severe in ash-exposed fish as sprint distance increased (30%, 57%, and 104% at 5, 10, and 20 cm, respectively; Figure 1). Neither condition factor nor nonpolar lipid content of fish influenced speed at any sprint distance (in all cases: $-0.13 \leq r_s \leq 0.51$, $p \geq 0.131$). Based on our ranks of fin erosion severity, caudal fin deterioration also had no effect on sprint speed at any distance measured ($-0.44 \leq r_s \leq 0.01$, $p \geq 0.170$). There was no relationship between sprint speed and the order of the sprint within each individual's replication sequence; in some cases peak velocity occurred during the first few sprints, and in others peak velocity was attained in the last few sprints.

Critical swimming speed was influenced by the interaction between fish standard length and sediment type (Table 3; Figure 2). Mean (± SE) U_{crit} of control and ash-exposed fish was 47.91 ± 3.62 and 24.02 ± 4.29, respectively. Linear regression indicated a positive relationship between fish standard length and U_{crit} among fish in the control treatment ($r^2 = 0.52$; $p = 0.028$), whereas there was no relationship between standard length and U_{crit} among fish exposed to ash ($r^2 = 0.29$; $p = 0.132$). Linear regression also indicated a positive relationship between fish mass and U_{crit} among fish in the control treatment ($r^2 = 0.47$; $p = 0.041$), whereas mass of fish

Table 1. Trace element concentrations (mean ± SE) in water, sediments, and whole bodies of lake chubsuckers (*Erimyzon sucetta*) from experimental tanks containing either coal ash-contaminated sediments (ash) or sand from a reference site (control)

	Water (ppb)		Sediments (ppm)		Fish (ppm)	
	Control	Ash	Control	Ash	Control	Ash
As	2.51 ± 0.24	38.67 ± 4.45	0.06 ± 0.02	52.10 ± 6.41	0.48 ± 0.13	1.45 ± 0.23
Cd	0.05 ± 0.01	0.31 ± 0.13	BDL	0.12 ± 0.02	0.08 ± 0.01	0.07 ± 0.01
Cu	2.20 ± 0.17	2.14 ± 0.41	0.53 ± 0.31	71.87 ± 3.19	4.12 ± 0.43	5.37 ± 0.32
Se	BDL	67.61 ± 19.84	BDL	6.56 ± 1.07	0.99 ± 0.03	3.80 ± 0.63
Sr	43.95 ± 2.17	463.18 ± 33.41	0.68 ± 0.12	235.97 ± 26.77	122.61 ± 13.73	215.24 ± 23.82
V	BDL	38.23 ± 10.894	0.32 ± 0.06	56.30 ± 6.04	0.87 ± 0.61	6.67 ± 1.40

Concentrations in sediments and fish are expressed as ppm dry mass. Concentrations below instrument detection limits are labeled BDL. Minimum instrument detection limits for As, Cd, Cu, Se, Sr, and V were 0.028, 0.001, 0.007, 0.097, 0.001, 0.018 ppb, respectively.

Table 2. Results of repeated-measures ANOVA of the effects sediment type and sprint distance on the sprint speed of lake chubsuckers (*Erimyzon sucetta*) exposed for 78 days to either contaminated or control sediments

Source	DF	MS	*F*	*p*
Among fish				
Sediment	1	0.7367	42.60	<0.001
Fish within sediment (error)	19	0.0173		
Within fish				
Distance	2	0.2513	38.43	<0.001
Distance × sediment	2	0.0538	8.22	0.001
Error (distance)	38	0.0065		

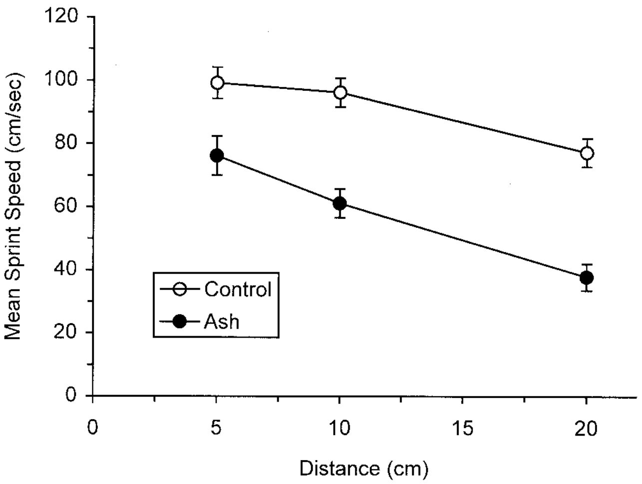

Fig. 1. Sprint speed (cm/s; mean ± SE) of lake chubsuckers (*Erimyzon sucetta*) exposed for 78 days to sand from a reference site (control) or contaminated sediments from coal ash disposal site (ash). Sprint speed was measured at three distances (5, 10, and 20 cm)

exposed to ash had a negative relationship with U_{crit} ($r^2 = 0.48$; $p = 0.039$). Fish condition factor did not influence U_{crit} in ash or control fish ($r_s = -0.55$ and -0.17, $p = 0.125$ and 0.668, respectively). Percent nonpolar lipid did not influence U_{crit} in ash or control fish ($r_s = 0.55$ and 0.05, $p = 0.160$ and 0.911, respectively). Furthermore, caudal fin deterioration had no effect on U_{crit} among ash-exposed fish ($r_s = -0.04$, $p = 0.786$).

Table 3. Results of ANCOVA investigating differences in the relationship of standard length and critical swimming speed between fish exposed to contaminated and control sediments for 90–100 days

Source	DF	MS	*F*	*p*
Sediment	1	720.435	7.26	0.017
Mass	1	20.619	0.21	0.656
Sediment × mass	1	880.272	8.87	0.010
Error	14	99.219		

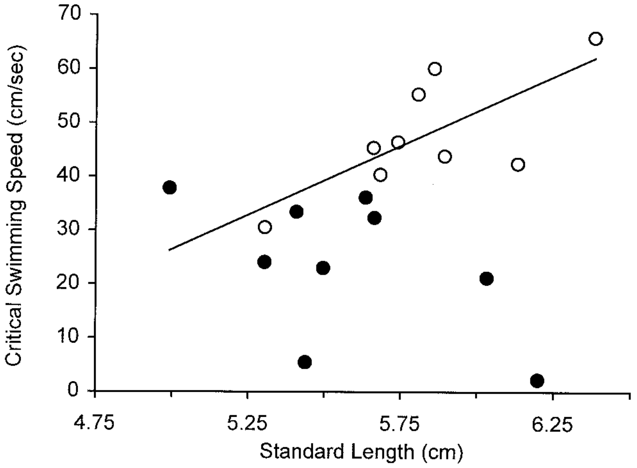

Fig. 2. Relationship between fish standard length (cm) and critical swimming speed (U_{crit}; cm/s) of lake chubsuckers (*Erimyzon sucetta*) exposed for 90–100 days to sand from a reference site (open symbols; solid line) or contaminated sediments from coal ash disposal site (shaded symbols). Regression results were: control, $y = 25.87x - 102.85$; $r^2 = 0.52$, $p = 0.028$; ash, $y = -19.00x + 129.92$; $r^2 = 0.29$, $p = 0.132$. Only the regression for the control fish is shown on the graph

Discussion

Benthic fish exposed to ash in the laboratory accumulated trace elements and exhibited significant reductions in swimming performance. Concentrations of As, Se, Sr, and V accumulated by fish greatly exceeded controls and were comparable to levels previously documented in chubsuckers exposed to ash (Hopkins *et al.* 2000a, 2002). Most fish accumulating trace elements otherwise had normal body composition (*i.e.*, % lipid stores), condition factors, and survival, yet sublethal toxicity was clearly manifest in compromised sprint speed and U_{crit}. Thus performance measurements were much more sensitive endpoints of ash toxicity than mortality or measures of condition. Such results are particularly important because concentrations of some trace elements accumulated by ash-exposed fish were below recommended toxicity thresholds (*e.g.*, Se reproductive toxicity threshold: 4 ppm whole body dry mass; Lemly 1996), suggesting that impairment of performance may be a more sensitive indication of fish health than more traditional toxicity endpoints (Schreck 1990; Little and Finger 1990).

Sprint speed of control fish was within the broad range of sprint and burst velocities documented for other fish species (Beamish 1978), but conspecifics exposed to ash exhibited significant reductions in sprint velocity at all three sprint distances. As expected, sprint speed decreased significantly as sprint distance increased, but the effect of distance was most pronounced in ash-exposed fish. As sprint distance increased from 5 to 20 cm, the percent difference in sprint velocity between sediment treatments tripled. Such pronounced reductions in sprint capacity could have important implications for inter- and intraspecific ecological interactions. For example, previous studies indicate that bullfrog larvae (*Rana catesbeiana*) exposed to ash exhibited similar reductions in sprint performance (Raimondo *et al.* 1998; Hopkins *et al.* 2000b) and were more frequently ingested by predators compared to unexposed conspecifics (Raimondo *et al.* 1998). Future studies that evaluate interactions between predators and ash-exposed chubsuckers with compromised sprint capacity would be valuable for determining the ecological significance of our findings.

Critical swimming speed of lake chubsuckers from the control treatment were within the large range of values reported for other small fish (Beamish 1978; Cripe *et al.* 1984; Stobutzki and Bellwood 1994; Kolok and Oris 1995; Alsop and Wood 1997; Farrell *et al.* 1997; Peake *et al.* 1997; Stevens *et al.* 1998; Gregory and Wood 1999), but were greatly reduced in fish exposed to ash. Although the U_{crit} of control lake chubsuckers (48 cm/s) exceeded many values reported for juvenile salmonids (range reported 36–54 cm/s), our findings were similar to values reported for representative species within Cyprinodontidae (Cripe *et al.* 1984), Cyprinidae (Nelson and Snodgrass in preparation), Atherinidae (Hartwell and Otto 1991), and Pomacentridae (Stobutzki and Bellwood 1994). In contrast to control fish, mean U_{crit} was nearly 50% lower in ash-exposed fish. Moreover, the typical positive relationship between U_{crit} and fish standard length (Beamish 1978; Nelson 1989; Farrell *et al.* 1997) was present among control fish but absent in fish exposed to ash. Such findings could have important implications for activities that require endurance. For example, lake chubsuckers are one of the most efficient colonizing species of isolated wetlands on the southeastern U.S. coastal plain (Snodgrass *et al.* 1996). Navigating the temporary connections between wetlands that periodically form during heavy rain events might require sustained locomotion, and such dispersal capacity could be compromised by exposure to contaminants.

Reductions in swimming performance following exposure to ash could not be attributed to pollutant-induced changes in condition factor, lipid storage, or fin erosion. Condition factor was normal (compared to controls) in fish exposed to ash and was not significantly correlated with sprint speed or U_{crit}. Other investigators have also found that condition factor does not influence U_{crit} (Kolok and Oris 1995; Gregory and Wood 1999). Similarly, there was no difference in percent nonpolar lipid in fish between treatments, and lipids were not correlated with swimming performance. This finding was in contrast to the work of Beamish *et al.* (1989), who found a significant negative relationship between whole-body lipid content and U_{crit} in juvenile lake trout. Such a discrepancy between studies could simply relate to the narrow range of lipid concentrations found in chubsuckers (resulting from provisioning of ample high-quality food) compared to the broader range reported by Beamish *et al.* (1989). Unlike condition factor and lipid composition, caudal fin morphology was significantly affected by ash exposure. Although 80% of fish exposed to ash had caudal fin erosion, severity of fin erosion (*i.e.*, fin erosion rank) did not relate to performance. Other studies examining the effects of fin damage on swimming endurance support our finding (Webb 1973; Gregory and Wood 1999). Webb (1973) found partial caudal fin amputations on sockeye salmon (*Oncorhynchus nerka*) did not decrease swimming endurance, leading to the conclusion that the caudal fin was more important for maneuverability than for speed or endurance. Because maneuvering is obviously critical for many aspects of fish biology, fin erosion caused by exposure to ash could have important implications for activities dependent on maneuverability (*e.g.*, predator avoidance).

Determining the physiological mechanisms by which ash disrupts swimming performance was beyond the scope of this study, but several physiological processes may be promising areas for further research. Burst and prolonged activities are regulated by different physiological processes and may therefore be disrupted by ash via different physiological mechanisms. Because burst activities occur rapidly over short distances, sprint performance would likely be influenced most by alterations to intramuscular creatine phosphate and ATP stores, anaerobic metabolism, and/or neuromuscular signaling (Schreck 1980; Weber and Spieler 1994; Garenc *et al.* 1999; Beauvais *et al.* 2000). In contrast, prolonged swimming activities (*e.g.*, U_{crit}) would likely be sensitive to changes in maximal aerobic capacity, cardiac output, function of red and white muscle fibers, as well as anaerobic metabolism (Farlinger and Beamish 1977; Beamish 1978; Thorarensen *et al.* 1996; Alsop and Wood 1997; Burgetz *et al.* 1998). Quantification of maximum aerobic capacity requires particular attention, as U_{crit} is equated with aerobic scope in most species examined to date. Decreased swimming performance may be the result of competing aerobic demands, such as detoxification, resulting in reduced scope for activity (Beamish 1978; Alsop and Wood 1997; Gregory and Wood 1999). In addition, aerobic capacity might be reduced if oxygen uptake and/or transport to tissues is reduced by contaminant exposure. Trace elements can alter gill tissue morphology resulting in impaired oxygen delivery to tissues during exercise (Mallatt 1985; Wilson *et al.* 1994). Sublethal exposure to trace elements can also result in elevated hemoglobin and plasma protein concentrations, leading to hemoconcentration and local tissue hypoxia (Randall and Brauner 1991; Beaumont *et al.* 1995).

Taken together, the results of our studies (current study; Hopkins *et al.* 2000a, 2002) suggest that measures of fish swimming performance are extremely sensitive indicators of health in ash-exposed fish. We found that some individuals exposed to ash appeared outwardly healthy (had normal body size, condition, and little fin erosion) but actually had the poorest swimming performance. Such sublethal changes could have important implications for the fitness of affected individuals, and perhaps ultimately contribute to the altered aquatic community structure found in ash-impacted sites (*e.g.*, Belews Lake, NC; Lemly 1993). Future studies that evaluate the effects of altered swimming performance on community interactions (*e.g.*, predator–prey dynamics) will aid in elucidating the ecological importance of our findings.

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