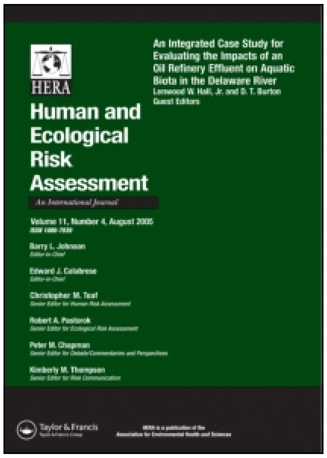

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Copper-Impaired Chemosensory Function and Behavior in Aquatic Animals

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ABSTRACT

Chemosensation is one of the oldest and most important sensory modalities utilized by aquatic animals to provide information about the location of predators, location of prey, sexual status of potential mates, genetic relatedness of kin, and migratory routes, among many other essential processes. The impressive sophistication of chemical communication systems among aquatic animals probably evolved because of the selective pressures exerted by water as a "universal solvent." Impairment of chemosensation by toxicants at the molecular or cellular level can potentially lead to major perturbations at higher levels of biological organization. We have examined the consequences of metal-impaired chemosensory function in a range of aquatic animals that represents several levels of a typical aquatic ecosystem. In each case, low, environmentally relevant metal concentrations were sufficient to cause chemosensory dysfunction. Because the underlying molecular signal transduction machinery of chemosensory systems demonstrates a high degree of phylogenetic conservation, we speculate that metal-impaired chemosensation among phylogenetically disparate animal groups probably results from a common mechanism of impairment. We propose developing a chronic chemosensory-based biotic ligand model (BLM) that maintains the advantages of the current BLM approach, while simultaneously overcoming known difficulties of the current gill-based approach and increasing the ecological relevance of current BLM predictions.

Key Words: *Daphnia*, leeches, fish, chemosensory dysfunction, metals.

INTRODUCTION

Animals participate in three major processes over the course of their lives: eating, avoiding being eaten, and reproducing (Wisenden 2000). Chemical information is used to make crucial decisions in each of these processes, particularly in aquatic systems. Aquatic animals also utilize chemical information to recognize kin (Olsen *et al.* 1998; Courtenay *et al.* 2001; Olsen *et al.* 2002), determine migratory routes (Li

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et al. 1995; Bjerselius *et al.* 2000), and evaluate their environment against several important criteria (Hara 1975). Each of these activities is critical for survival. Consequently, anything that could impair an aquatic animal's ability to perceive important chemical information could have significant ecological ramifications. It has long been known that copper, at relatively high aqueous concentrations, can temporarily impair olfaction in fish (reviewed in Klaprat *et al.* 1992). The mechanism of copper impairment of fish olfaction is unknown. Although some attention has been paid to understand the effects of metals on fish olfaction, little is known about the ecological consequences of metal-impaired chemosensation in fish, and whether or not this impairment extends to other aquatic animals. Moreover, previous studies examining effects of metals on chemosensation have been conducted primarily under controlled laboratory conditions and do not necessarily reflect natural contaminant-exposure conditions.

This article represents a summary of work conducted in our laboratory—including both published and unpublished results—investigating the effects of metals on chemosensory function of aquatic animals representing three trophic levels typical of northern freshwater systems: *Daphnia pulex* represents zooplankton; *Nephelopsis obscura* represents the benthos; and two fish species, fathead minnows (*Pimephales promelas*) and Iowa darters (*Etheostoma exile*) represent secondary consumers. The purpose of this article is to demonstrate the extent to which dissolved waterborne copper influences chemosensory function at different representative trophic levels of a typical aquatic ecosystem, and to highlight subtle effects of copper exposure that could potentially yield important ecological consequences.

Chemosensation in Aquatic Animals

Daphnia pulex–Chaoborus americanus predator–prey system

The water flea, *D. pulex,* is a common zooplankton species in freshwater lakes that occupies an important trophic position as a primary consumer. Phantom midge, *Chaoborus americanus,* larvae are gape-limited predators that feed on *D. pulex* neonates. *Chaoborus* actively feeding on *D. pulex* release a predator kairomone from their digestive tracts that induces the production of neck spines in the first through third instar in *D. pulex* (Krueger and Dodson 1981; Vuorinen 1989; Lüning 1992). Kairomone-induced neck spines serve to increase the size of *D. pulex* neonates beyond the gape limit of *C. americanus* causing a reduction in the latter's handling efficiency of the former during a predatory attack (Krueger and Dodson 1981). In a properly functioning system, neck spine induction increases survival by up to 67% (Krueger and Dodson 1981; Havel and Dodson 1984; Spitze and Sadler 1996). Because the predator–prey relationship between *C. americanus* and *D. pulex* is mediated through chemosensory detection of the predator kairomone (Kats and Dill 1998; Tollrian and Dodson 1999; Lass and Spaak 2003), it is possible that dissolved metals may interfere with neck spine induction in *D. pulex,* which could lead to a corresponding increase in predation vulnerability.

Leeches—Nephelopsis obscura

Leeches are both benthic predators and an important food source for fish in most freshwater systems. Consequently, like *Daphnia,* leeches occupy an important trophic position in aquatic ecosystems. Foraging by leeches involves either active stalking using complex search patterns (Davies *et al.* 1982), or a more passive sit-and-wait approach (Wrona and Calow 1988). In either case, leeches rely on chemosensation to locate potential food sources. This is evidenced by the development of specialized chemoreceptors, which are found in three different areas of the leech body: (i) spread diffusely over the body; (ii) surrounding the dorsal lip; and (iii) in a specialized chemosensory epithelium lining the gut to facilitate post-ingestive food sampling (Elliot 1987; Kornreich and Kleinhaus 1999).

Chemosensory function has only been studied in a few leech taxa, primarily the blood-sucking leeches *Hirudo, Macrobdella,* and*Haemopsis* spp. (Kornreich and Kleinhaus 1999). However, this specialized sensory system may be more widespread among other leeches as well (Simon and Barnes 1996). Because of this specialized chemosensory system, disruption of chemosensation can potentially lead to significant ecological effects.

Nephelopsis obscura is a predatory leech found in most freshwater systems of North America. It is currently unknown to what extent *N. obscura* relies on chemosensation to locate its prey. However, as with most other aquatic organisms, chemosensation plays an important role in prey location leading us to believe that it plays a role in *N. obscura* as well. To examine this more closely, we tested the role of chemosensation in prey location. We conducted a series of experiments, reported later in this article, which explicitly tested the role of chemosensation in *N. obscura* to locate food, avoid copper contaminated food, and to determine if exposure to waterborne copper influenced these abilities.

Fish—Secondary Consumers

Aquatic animals also use chemical information to avoid predators (*e.g.*, alarm cues). Natural selection has favoured the ability of receivers to recognize and respond appropriately to these cues as needed. Numerous studies have shown the importance and sophistication of how chemical information is used in these processes (Chivers and Smith 1998; Kats and Dill 1998; Stacey 2003; Sorensen and Stacey 2004). Disruption of chemical cue perception can be detrimental to the individual and result in effects that can become manifest at the population, community, or ecosystem levels.

Several taxonomically distinct groups of fish use chemical alarm cues to assess predation risk (reviewed in Smith 1992; Chivers and Smith 1998). Chemical alarm cues can fall into one of four categories: (i) predator odors; (ii) disturbance cues (nitrogen based compounds); (iii) damage-released alarm cues (mechanical damage to prey); and (iv) diet cues (cues released as prey are digested). Upon detection of these cues, prey exhibit a number of typical antipredator responses which include area avoidance, decreased activity, decreased foraging, and increased group cohesion (Lima and Dill 1990).

Two previous studies have tested the responses of fish to damage-released alarm cues after exposure to waterborne metals. Beyers and Farmer (2001) exposed Colorado pikeminnows (*Ptychocheilus lucius*; Cyprinidae) to six nominal copper concentrations ranging from <10 to 266 μg Cu/L for 24 h and 5 nominal copper concentrations ranging from <10 to 129 μg/L for 96 h. They found that fright responses of pikeminnows decreased with increasing copper concentration. Moreover, fish exposed to copper for 24 h exhibited stronger olfactory sensitivity than those exposed for 96 h. Similarly, Scott *et al.* (2003) found that rainbow trout (*Oncorhynchus mykiss*) exposed to 2 μg Cd /L (nominal) for 7 d exhibited no fright response to rainbow trout alarm cue compared to controls. Interestingly, they also found that after 3 and 5 d exposures the olfactory rosette accumulated 7 times more cadmium than the liver and 5 times more after a 7 d exposure. These studies suggest that olfactory disruption occurs quickly after exposure and that physiological protection mechanisms may also be initiated immediately.

Although these studies suggest that olfactory impairment occurs in fish exposed to waterborne copper concentrations, the effect appears to be transient—at least in adults. Olfactory receptor neurons are the only vertebrate neurons capable of division (Laberge and Hara 2001). Consequently, fish experiencing copper-induced olfactory impairment can recover over a relatively short period of time in clean water. One question that remains is whether or not developing fish embryos experience copper-impaired olfaction, and if they do, whether or not this impairment is permanent or transient.

Finally, most of the research demonstrating metal-impaired olfaction in fish has been conducted under tightly controlled laboratory conditions. It is currently unknown if fish inhabiting metal-contaminated environments adapt to elevated waterborne metal concentrations, or if the effects observed under laboratory conditions can be extrapolated to natural environments.

MATERIALS AND METHODS

Zooplankton—*Daphnia pulex*

In order to examine the effects of environmentally relevant copper concentrations on *Chaoborus americanus* kairomone-induced neck spine induction in *Daphnia pulex*, we exposed individual adult *D. pulex* to 4 increasing nominal copper concentrations ranging from 0 μg/L to 25 μg/L in the presence of one of three chemical stimuli: dechlorinated municipal tap water, DW (a neutral control); water conditioned by *C. americanus* fed *Artemia salina*, K(−) (control for a general diet cue); or water conditioned by *C. americanus* fed *D. pulex*, K(+) (predator kairomone to which we expected neck spine induction) (Hunter and Pyle 2004). Therefore, this experiment was conducted as a full 4 (copper concentrations) × 3 (stimuli) × 4 (replicates) factorial design. Test subjects (adult *D. pulex*) were held under these conditions for up to 22 days, during which time neonates were removed and examined daily for the presence of neck spines (counting and measuring the length using a compound microscope fitted with an ocular micrometer). Full methodological details can be found in Hunter and Pyle (2004).

Benthos—Leeches

In the first experiment, we tested leeches for their ability to detect and locate food through chemosensation. To test the effect of waterborne copper on *Nephelopsis obscura*'s ability to detect and respond to chemical food cues, we exposed 50 leeches to one of three nominal waterborne copper concentrations (0, 10 and 20 μg /L), and tested their individual response to a food stimulus in a Y-maze after 0, 2, 4, 8, and 16 d of copper exposure ($n = 10$). One arm of the Y-maze received beef liver homogenate (food source) at a rate of 1 mL/min., whereas the other arm received a water blank (control) delivered at the same rate. Leeches were selected randomly for behavioral testing from among the three copper treatments, and the stimulus assigned to each arm of the Y-maze was randomized from one trial to the next. Leeches were allowed to acclimate to the Y-maze testing conditions for 8 min before the food stimulus was delivered to one arm of the maze and the control stimulus was delivered to the other arm. Leeches were then observed for another 8 min, and their position in one arm or the other of the Y-maze was monitored continuously throughout the 8 min post-stimulus delivery period. All trials were conducted in clean water.

In a second experiment, we examined the effects of copper on leech feeding activity by testing the amount of time it took for leeches to locate a food source (a dead fathead minnow) in a small fingerbowl, and once found how long they remained attached and actively feeding. Leeches were exposed to 0, 5, or 10 μg Cu/L for 8 d. Similarly, fathead minnows were also exposed to 0 or 10 μg Cu/L for 8 d to represent clean and contaminated food sources. Individual leeches were randomly selected from each of the three copper-exposure treatments and were placed in a small fingerbowl with a single dead minnow for 10 min. During each trial, total time swimming (searching), total time attached to the minnow (feeding) was recorded (n = 18–20). The number of individual leeches demonstrating an aversion response, defined as a rapid writhing behavior or by attempting to escape the trial arena, was also recorded.

Secondary Consumers—Fish

Previous studies have demonstrated that environmentally relevant copper concentrations can impair olfaction in fish, and that this impairment is transient in adult fish. In this study, we wanted to determine if long-term chemosensory deficits occur when fish are exposed to copper during a sensitive, developmental life stage. Carreau and Pyle (2005) exposed freshly fertilized fathead minnow embryos to either 0 or 10 μg Cu/L (nominal) until they hatched 5–7 d later. Upon hatching, larvae were randomly assigned to one of three experimental treatments for 84–96 d: (i) larvae exposed to 0 μg Cu/L as embryos were placed in clean water (0 μg Cu/L); (ii) larvae exposed to 10 μg Cu/L as embryos were placed in either a 10 μg Cu/L solution; or (iii) clean water, 0 μg Cu/L. At the end of this 84–96 d post-hatch exposure period, juvenile minnows were tested in a triumvirate maze for their responses to three different chemical stimuli ($n = 10$): (i) fathead minnow alarm cue; (ii) swordtail (*Xiphophorus helleri*) skin extract; or (iii) a blank water control. Swordtail skin extract controls for generalized responses to an injured fish. Full methodological details can be found in Carreau and Pyle (2005).

To determine if the metal-induced chemosensory deficits observed under laboratory conditions extrapolate to natural environments, we conducted a field test to determine whether fish could avoid alarm cues in the wild in clean and metal contaminated lakes (McPherson *et al.* 2004). We chose Iowa darters, *Etheostoma exile*, as our test species because they were common to both of our test lakes: Kelly Lake in the industrial region of Sudbury, ON (metal contaminated), and James Lake near North Bay, ON (reference lake). We placed 20 sets of three minnow traps in each lake for 10 h. Each trap contained a 1 cm^3 cellulose sponge saturated with either: (i) Iowa darter alarm cue; (ii) swordtail skin extract; or (iii) distilled water. After 10 h the traps were pulled and the number of darters enumerated. Specific methodological details can be found in McPherson *et al.* (2004).

RESULTS AND DISCUSSION

Zooplankton—*Daphnia pulex*

Daphnia pulex exposed to K(+) in clean water produced at least twice as many neck spines than those exposed to either K(−) or DW controls ($F_{2,8} = 11.8$, $p = 0.004$; Figure 1). However, *D. pulex* exposed simultaneously to K(+) and copper, at all copper concentrations tested, produced the same number of neck spines as the K(−) and DW controls, indicating that even low copper concentrations are enough to impair neck spine induction. Although the number of kairomone-induced neck

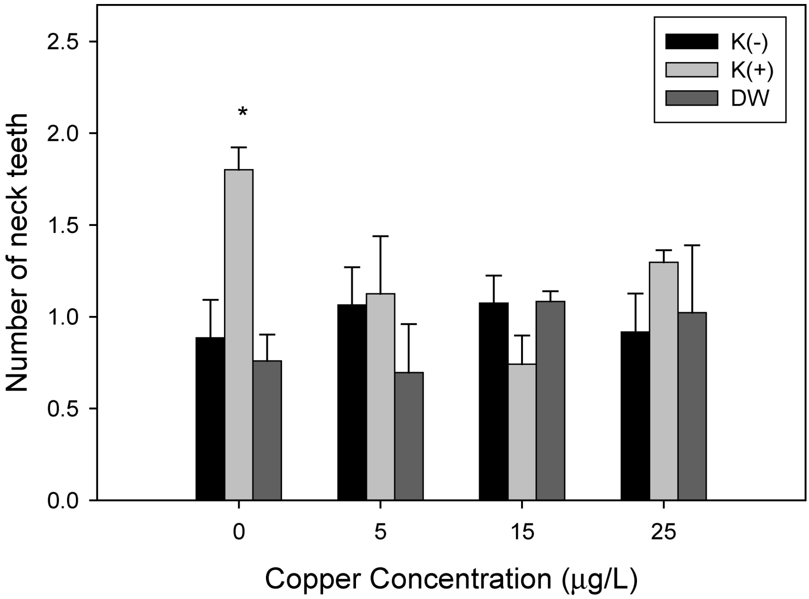

Figure 1. Effect of copper on *Daphnia pulex* neonate neck spine production in the presence of dechlorinated municipal tap water (DW), water conditioned by *Chaoborus americanus* feeding on *D. pulex* [K(+)], or *C. americanus* feeding on *Artemia salina* [K(−)], Data are presented as means + SEM ($n = 4$) neck spine number. * indicates significant difference from DW and K(−), $p < 0.05$. Copyright © Society of Environmental Toxicology and Chemistry, from Hunter and Pyle (2004). Reprinted by permission of Alliance Communications Group, a division of Allen Press, Inc.

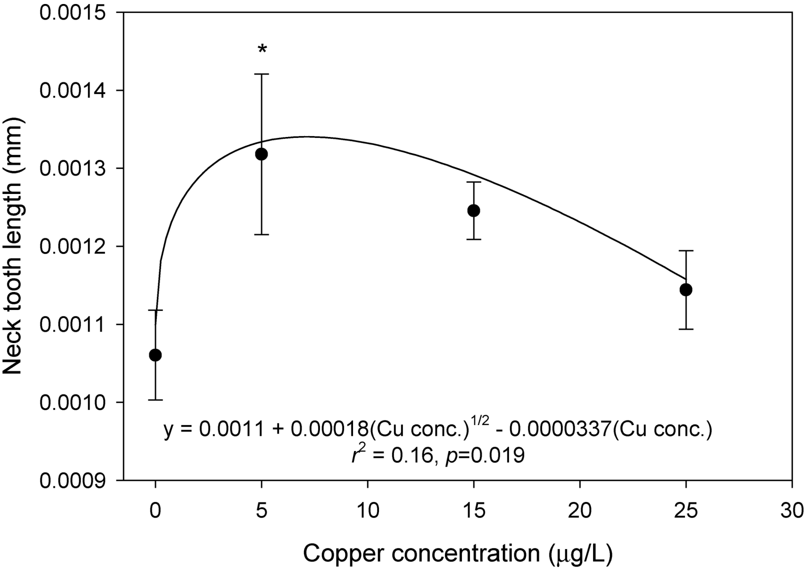

Figure 2. Effect of copper on *D. pulex* neck spine length. Data are presented as means ± SEM ($n = 12$). * indicates significant difference from 0 μg/L Cu ($p < 0.05$). Copyright © Society of Environmental Toxicology and Chemistry, from Hunter and Pyle (2004). Reprinted by permission of Alliance Communications Group, a division of Allen Press, Inc.

spines was significantly reduced at 5 μg Cu/L, neck spine length increased ($F_{3,44} = 2.87$, $p = 0.047$; Figure 2). However, at higher copper concentrations neck spine lengths were not significantly different than those measured in *D. pulex* in clean water.

Together, these results suggest that there are possibly two related signal transduction pathways that mediate the response to predator kairomone in *D. pulex*: one that regulates the number of neck spines and another that regulates their length. Because neck spine length was increased at 5 μg Cu/L, we speculate that the kairomone signal was at least partially perceived by *D. pulex*. This result suggests that at low copper concentrations, the pathway leading to neck spine number is impaired, while that leading to neck spine length is enhanced. At higher copper concentrations, both pathways are impaired, suggesting that the mechanism of copper inhibition of chemosensation in *D. pulex* probably involves inhibition somewhere along the molecular signal transduction cascade.

That neck spine induction was inhibited at all copper concentrations tested suggests that in natural systems contaminated by copper, *D. pulex* may be more susceptible to predation by *C. americanus* than daphnids living in clean environments. The potential ecological perturbation that may result, given *D. pulex*'s important trophic position as a primary consumer, is currently unknown and warrants further investigation.

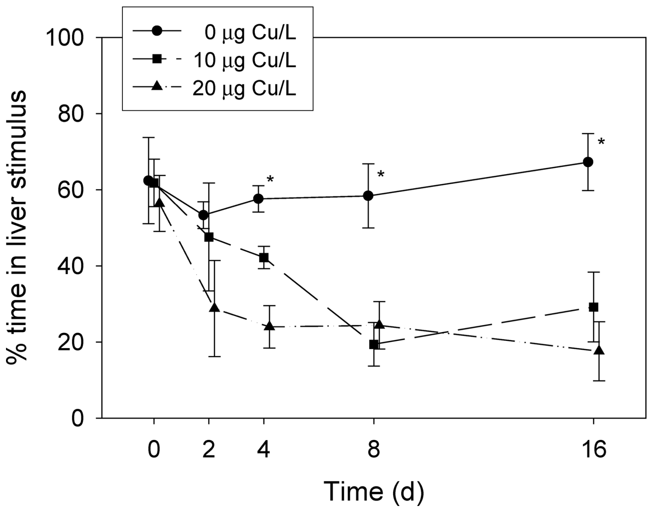

Figure 3. Time spent by freshwater leeches, *Nephelopsis obscura*, in an arm of a Y-maze receiving a food stimulus (beef liver homogenate) after 0–16 d exposure to one of three concentrations of waterborne copper. Data are represented as means ± SEM ($n = 10$) proportion (%) of total time spent in all arms of the maze (points are artificially offset for clarity). * indicates significant difference of leeches exposed to 10 or 20 μg Cu/L from those exposed to 0 μg Cu/L ($p < 0.05$).

Benthos—Leeches

After 4 d, leeches held in both the 10 and 20 μg Cu/L exposures spent significantly less time in the Y-maze arm receiving the food cue than leeches held in clean water, and those held at 10 μg Cu/L spent about twice as much time in the food cue arm than those held in 20 μg Cu/L ($F_{2,27} = 16.5, p < 0.0001$; Figure 3). By day 8, leeches held in either copper-exposure spent approximately 30% of their time in the food-cue arm relative to controls, who spent approximately 60% of their time in the food cue ($F_{2,27} = 9.5, p = 0.0008$). This effect persisted through 16 d of copper exposure ($F_{2,27} = 4.0, p = 0.03$).

In the second experiment, leeches exposed to copper spent significantly more time searching for the food ($F_{2,54} = 5.42, p = 0.007$), and less time feeding ($F_{2,54} = 3.24, p = 0.047$), than those held in clean water (Figure 4). Moreover, leeches held in clean water for 8 d showed a clear aversion response to the contaminated food source ($\chi^2 = 7.34, p = 0.007$; Table 1). Leeches exposed to water containing more than 5 μg/L did not demonstrate any significant aversion to the contaminated food source than did those presented with a clean food source ($\chi^2 < 1.34, p > 0.05$; Table 1).

These data suggest that copper has an important deleterious effect on chemosensory function in leeches. Leeches exposed to relatively low waterborne copper concentrations are unable to detect food cues or to discriminate between clean or metal-contaminated food sources. This could lead to an increased risk of starvation, or increased dietary exposure to potentially toxic metals in leeches inhabiting

Table 1. Summary of contingency analyses examining the proportion of individual leeches ($n = 18$–20) exposed to 0, 5, or 10 μg Cu/L demonstrating an aversion response (defined as vigorous writhing or "knotting" or attempting to escape the trial arena) to a clean or metal contaminated food source (dead fathead minnow held for 8 d in clean water or water containing 10 μg Cu/L, respectively).

Leech exposure (μg/L)	Food exposure (μg/L)	No aversion (%)	Aversion (%)	χ^2	p
0	0	45.0	0.0	7.34	0.007
	10	30.0	25.0		
5	0	47.4	0.0	~0.00*	~1.00
	10	52.6	0.0		
10	0	33.3	16.7	1.33	0.25
	10	44.4	5.6		

*No leech demonstrated an aversion response, regardless of food contamination level, when leeches were exposed to 5 μg/L. Therefore, χ^2 approached zero and could not be calculated directly.

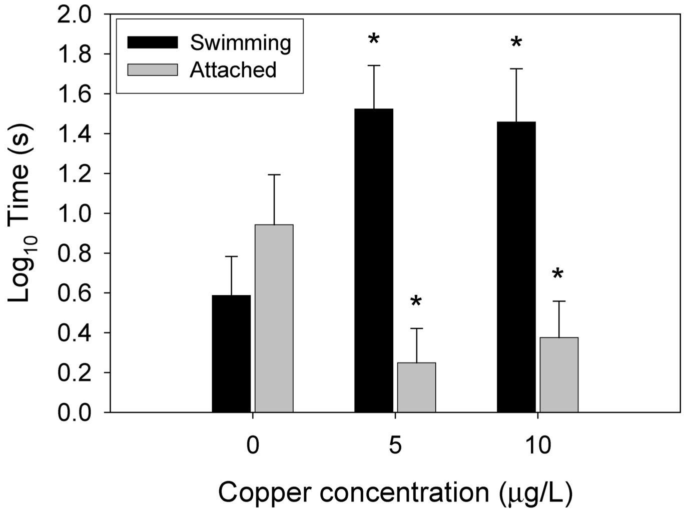

Figure 4. Effect of waterborne copper exposure on the feeding activity of freshwater leeches, *Nephelopsis obscura,* when presented with food (dead fathead minnow) in a small fingerbowl. "Swimming" represents the amount of time the leech spent searching for the food source. "Attached" represents the amount of time the leech spent attached to the food source actively feeding. Data are represented as mean ± SEM ($n = 18$–20); * indicates significant difference from 0 μg Cu/L for similarly shaded bars ($p < 0.05$).

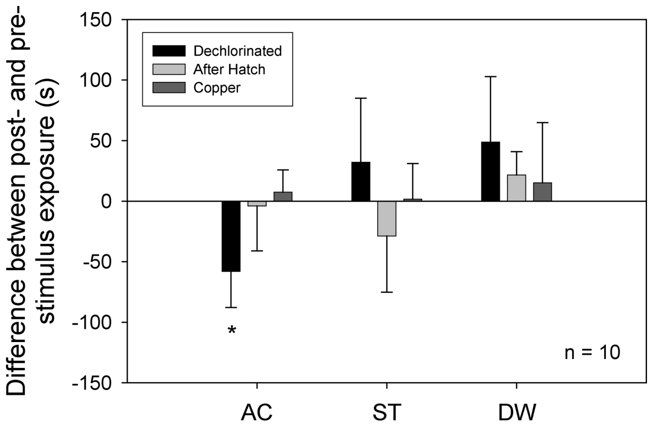

Figure 5. Effect of copper exposure to fathead minnow embryos on their ability to respond to conspecific alarm cue (AC), swordtail skin extract (ST), or dechlorinated water (DW) 84–96 d post-hatch. "Dechlorinated" refers to exposure to clean water during both developmental and post-hatch periods. "After hatch" refers to embryos exposed to 10 μg Cu/L only during the developmental period, and clean water during the post-hatch period. "Copper" refers to fish held in 10 μg Cu/L water during both the developmental and post-hatch periods. Negative values indicate avoidance, positive values indicate attraction. * indicates significant difference from zero (difference between 8 min. post-stimulus and 8 min. pre-stimulus delivery periods; $p < 0.05$). Reprinted from Carreau and Pyle (2005) with permission from Elsevier.

metal-contaminated habitats. Given the leech's ecological importance in a freshwater system, metal-induced damage in leech chemosensation could lead to wider-scale ecological perturbations that warrant further study.

Fish—Secondary Consumers

Minnows held at 0 μg Cu/L during embryological development and during the post-hatch exposure period avoided the maze arm receiving conspecific alarm cue ($t = -1.96$, $d.f. = 9$, $p = 0.04$; Figure 5). However, minnows that were continually exposed to copper did not avoid the arm containing minnow alarm cue ($t = 0.40$, $d.f. = 9$, $p = 0.65$). Minnows that were only exposed to copper as embryos also did not avoid the arm of the maze containing minnow alarm cue ($t = -0.11$, $d.f. = 9$, $p = 0.46$). Not only does this study verify that waterborne copper exposure disrupts olfactory function, it also suggests that there is a sensitive developmental stage during which copper exposure impairs olfactory function which does not recover even after a 96 d post-hatch recovery period. In other words, copper may disrupt important developmental stages in the embryonic olfactory system that can translate to severe chemosensory impairment later in life. From an ecological risk management point of view, there may be some value to limiting the release of copper effluents to aquatic receiving environments during the periods of the year associated with fish spawning

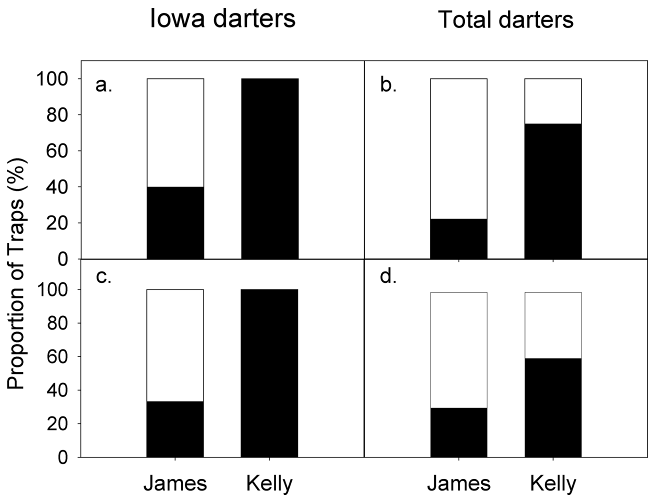

Figure 6. Wild darter response to Iowa darter alarm cues in a clean (James Lake) and a metal-contaminated lake (Kelly Lake). Black bars represent the proportion of traps treated with Iowa darter alarm cue that caught more or equal numbers of fish than traps treated with either distilled water (a, b) or swordtail skin extract (c, d) controls. White bars indicate the proportion of traps treated with Iowa darter alarm cue that caught fewer fish than either of the controls. Panels on the left represent the response of Iowa darters, whereas panels on the right represent the response of all darter species together. Data were analysed by contingency analysis. Responses in panels a, b, and c were significant ($p < 0.05$). Reprinted from McPherson *et al.* (2004) by permission from NRC Research Press.

activities. More work is required to understand the full ecological implications, and solutions to mitigate, these effects.

Previous studies that have tested the effects of copper on fish olfactory function were mostly conducted under tightly controlled laboratory conditions. To determine if these effects extend to natural environments, we conducted a field test to determine whether fish could avoid alarm cues in the wild in clean and metal contaminated lakes (McPherson *et al.* 2004). Iowa darters avoided traps treated with the alarm cue in the clean lake relative to a distilled water control, but not in the contaminated lake ($\chi^2 = 3.86$, $p = 0.02$; Figure 6a). Similarly, in the clean lake Iowa darters avoided traps treated with conspecific alarm cue relative to traps treated with swordtail skin extract, but not in the contaminated lake ($\chi^2 = 3.29$, $p = 0.03$; Figure 6b). This study confirms that even under natural conditions when exposed to a virtual cocktail of metal contaminants, olfactory function is impaired.

CONCLUSIONS

We have shown that copper can interfere with chemosensation in three representative levels of a typical aquatic ecosystem: the benthos, zooplankton (primary consumers), and fish (secondary consumers). Processes affected by waterborne metal impairment of chemosensation include defending against predation and finding food. We have also demonstrated that sex cue perception can be impaired in fish exposed to environmentally relevant waterborne copper concentrations (data not shown), which could lead to significant effects on reproduction. Moreover, these effects occur at concentrations lower than those known to induce acute toxicity, and effects observed under carefully controlled laboratory conditions were shown to occur in natural environments.

Although there is a wide diversity of chemosensory systems across animal phyla, the olfactory signal transduction cascade and corresponding physiological processing of odorant molecules shows a high degree of phylogenetic conservation among invertebrates and vertebrates (Hildebrand 1995; Krieger and Breer 1999; Firestein 2001). Therefore the mechanism by which copper is disrupting chemosensory function may be similar across taxa. We propose three hypotheses to explain these effects. First, copper may alter the chemical signal itself in the water column, thereby disrupting its ability to bind to the chemosensory receptor. Second, copper may compete with chemosensory molecules for binding sites on the sensory epithelium. Third, copper may act on the molecular signal transduction pathway inhibiting the signal from being propagated from the sensory epithelium to the brain. Our data suggest that the third hypothesis is most likely and work is currently underway to explore this possibility. Moreover, this impairment may occur at sensitive stages of development leading to chemosensory dysfunction that can persist to later life stages (Carreau and Pyle 2005).

Regardless of the proximate mechanism that disrupts chemosensory function we cannot overlook the ecological significance. The impairment of the ability to detect and utilize chemical information from the local environment may have significant consequences at the population and community levels of organization. If animals cannot locate food, identify appropriate mates, or avoid predators then drastic shifts in population numbers and species composition could result. These effects occur at all representative ecosystem levels that we tested, which suggests that metal-induced chemosensory dysfunction may be a widespread phenomenon.

Current ecological risk assessments and environmental regulations have ignored metal effects on chemosensation, despite the possibility that these effects could translate into large-scale ecological perturbations. We propose the development of a chronic chemosensory-based Biotic Ligand Model (BLM) to overcome some known difficulties with the current BLM approach (including diet effects), and to increase the ecological relevance of toxicological predictions. This approach could potentially be extended over a wide range of animal species owing to the phylogenetic conservation of underlying signal transduction cascades among disparate animal phyla, and improve ecological risk assessments of metal-contaminated environments.

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