Ecological Applications, 20(8), 2010, pp. 2089–2095
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Blinded by the stink: Nutrient enrichment impairs the perception of predation risk by freshwater snails

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Abstract. The acquisition of sensory information is central to all species interactions. Most aquatic organisms use chemical cues to assess predation risk and other key ecological factors, but chemoreception may be disrupted in systems with elevated pH. Elevated pH in lakes and rivers is often associated with eutrophication. We used laboratory and mesocosm experiments to test whether elevated pH impairs perception of predation risk by the freshwater snails *Physa acuta* and *Helisoma trivolvis*. In one set of experiments, nutrients were added to outdoor mesocosms, resulting in mid-afternoon pH values of 8.5–9.7. Both snail species moved to avoid fish in water with pH < 9.0 but showed no avoidance at higher pH. In a laboratory study, we used buffers to establish six pH treatments ranging from 7.5 to 10.0. At lower pH *Physa acuta* responded to fish cues by moving into safer habitats, but avoidance became impaired at a pH of 9.4. *Helisoma trivolvis* also responded to fish at lower pH, and their avoidance behavior became impaired at a pH of 8.8. Given the diversity of aquatic organisms that depend on reception of chemical cues and the broad extent of eutrophication, chemosensory impairment is likely a common occurrence in nature.

Key words: chemoreception; eutrophication; inducible defenses; pH; phenotypic plasticity; predator avoidance; sensory impairment.

Introduction

Organisms assess critical features of the environment by gathering sensory information. Such information is vital to individual decision-making, and the choices mediated by sensory information have consequences that shape populations, communities, and ecosystems (Lima 1998, Agrawal 2001, Werner and Peacor 2003). Ultimately, the nature of species interactions depends in a fundamental way on the perception of sensory cues. In aquatic systems, chemoreception is the most prevalent mechanism by which plants and animals gather information from their surroundings (Brönmark and Hansson 2000, Hay and Kubanek 2002, Derby and Sorensen 2008). Thus, reception of chemical information may have large consequences for both individual fitness and community structure. Any disruption of chemical information transfer will likely reorganize the ecological community, but constraints on chemosensory reception have received little attention (Weissburg et al. 2002, Smee et al. 2008).

Recent literature shows that anthropogenic pollutants can disrupt chemoreception in lakes and streams, even when at low, non-toxic concentrations (Lurling and Scheffer 2007). Humans also have had a more subtle but pervasive effect on the chemistry of aquatic systems by alteration of hydrogen ion concentration (pH). Ocean acidification associated with increasing atmospheric concentration of carbon dioxide and acidification of lakes and streams by sulfur and nitrogen deposition are two well known examples. Chemoreception in fish (Smith and Lawrence 1988, Brown et al. 2002, Leduc et al. 2004) and crayfish (Allison et al. 1992) is impaired in weakly acidified streams. Similarly, marine fish reared in acidified seawater fail to respond appropriately to predator cues (Dixson et al. 2009).

Although the effects of acidification on chemoreception have received some attention, the effects of elevated pH on chemoreception are unstudied. High pH in nature is usually associated with nutrient enrichment (eutrophication), especially in poorly buffered lakes and ponds (Talling 1976, Morgan 1985, Maberly 1996). The overenrichment of surface waters with nutrients is a widespread environmental problem and is likely to intensify in coming decades (Carpenter et al. 1998, Smith et al. 1998). Because the regulation of pH in freshwater is primarily attributable to bicarbonate buffering, a change in the availability of dissolved inorganic carbon will influence pH. Additions of a limiting nutrient stimulate plant productivity, and high rates of photosynthesis can deplete dissolved inorganic carbon, which in turn elevates pH during daylight hours. Elevated pH may impair chemoreception by changing the conformation of olfactory cues or olfactory receptors, but this idea is untested.

Manuscript received 28 January 2010; revised 19 May 2010; accepted 4 June 2010. Corresponding Editor: M. J. Vander Zanden.

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PLATE 1. *Helisoma trivolvis* (left) and *Physa acuta* (right) are two of the most widespread and common gastropods in North America. They both use chemical cues to assess predation risk. In the presence of molluscivorous fish they move to safe habitats such as shallow water or the undersides of rocks and logs. Photo credit: A. M. Turner.

Here we investigate whether the ability of freshwater gastropods to detect predators is impaired at high pH induced by elevated ecosystem productivity. Freshwater pulmonate snails are abundant and important components of freshwater food webs (Brönmark et al. 1992, Turner and Montgomery 2009). They use waterborne chemical cues to detect predators and respond with a suite of behavioral, life-historical, and morphological defenses (Crowl and Covich 1990, Alexander and Covich 1991, Turner 1996, DeWitt 1998). We evaluated the effect of nutrient enrichment on the ability of the freshwater snails *Physa acuta* and *Helisoma trivolvis* (see Plate 1) to detect pumpkinseed sunfish predators (*Lepomis gibbosus*) in an outdoor mesocosm study. Using the same predator and prey species, we also directly tested the effects of elevated pH on predator avoidance in a laboratory study by using buffers to manipulate pH.

MATERIALS AND METHODS

Enrichment study

We manipulated ecosystem productivity in mesocosms ($1.3 \times 0.8 \times 0.3$ m deep) placed outdoors at the Pymatuning Laboratory of Ecology in northwestern Pennsylvania, USA. In early July of 2007, 24 mesocosms were arranged in two rows of 12, filled with 130 L of well water (total phosphorus < 10 μg/L, bromocresol green alkalinity $= 200$ mg/L $CaCO_3$), inoculated with lake water to facilitate establishment of zooplankton and algae, and covered with 50% shade cloth. Four levels of nutrient enrichment were established with phosphate additions. Ambient nutrient tanks received no phosphate, and low, medium, and high nutrient treatment tanks ($n = 6$ tanks per treatment) were enriched with 100, 200, and 400 μg/L phosphorus added as K_2HPO_4. Nitrogen was added as $NaNO_3$ so as to maintain a 16:1 molar ratio.

Behavioral assays testing treatment effects on anti-predator responses were conducted with two representative species of freshwater snail, *Physa acuta* and *Helisoma trivolvis*. Both species use chemosensory information to detect pumpkinseed sunfish (*Lepomis gibbosus*) predators (Turner 1996). Pumpkinseed sunfish are specialized molluscivores, and pulmonate snails typically respond to pumpkinseed cues by moving into safer microhabitats such as under substrates or to the water's surface (Turner 1996, Turner and Montgomery 2003). The full anti-predator response is induced only when predators have recently fed on conspecific prey (Turner 2008). Snails and pumpkinseeds were collected from local ponds and lakes and held in captivity with food until use in experiments. Snails were already acclimated to high pH, as the pH of the ponds and lakes they were collected from ranged between 9.0 and 9.4 at the time of collection. Mid-afternoon pH of the holding tanks ranged between 9.0 and 9.2.

Because fertilized mesocosms grew more periphyton, the effects of elevated pH on snail behavior are potentially confounded with differences in food avail-

ability. In order to standardize food availability, we transferred water into smaller food-free containers for short-term behavioral assays. Water from each of the 24 mesocosms was used to fill two polyethylene wash-tubs ($30 \times 45 \times 15$ cm deep), one of which subsequently was treated with predator cues and the other with well water control. Difference in habitat use between predator cue and control tubs shows the strength of predator cue effects, and each pair of tubs thus constitutes a single observation, yielding six replicate observations for each of the four nutrient treatments.

Assays were initiated by filtering water from mesocosms through a 153-μm plankton net and decanting 10 L into each tub. Ten snails were immediately stocked into each tub and allowed to acclimate for approximately 1 h prior to cue additions. Predator cues were generated by feeding 30 snails to a single pumpkinseed sunfish housed in a 200-L mesocosm. After two hours, 0.5 L of predator cue was transferred to each predator tub and an equal volume of aerated well water to each control tub. We added an elevated tile (7.5×7.5 cm) to each tub to serve as a refuge for snails. Snail habitat use was recorded once each hour for 3 hours following cue addition. We observed the number of snails using near-surface habitat (within 2.5 cm of the water's surface) and the number under the substrate, and summed the total for a measure of refuge use. For each pair of tubs, predator avoidance was calculated by subtracting the proportion of snails using refuge habitats in the control from the proportion using these habitats in the predator tub. We measured pH of the water in the tubs immediately after cue addition and at the conclusion of the behavioral observations (Double junction, temperature compensated electrode, calibrated daily with fresh buffers).

We conducted two iterations of the behavioral assay with *Physa acuta* and one assay with *Helisoma trivolvis*. The first assay, with *Physa acuta* (mean shell length = 6 mm), was conducted one week following fertilization. Eight days later we repeated the *Physa* assay, using the same set of 24 mesocosms but a fresh set of snails. The *Helisoma* behavioral assay (mean shell length = 6 mm) was conducted between the two *Physa* assays, and employed the same methods, except that predator cues were generated by feeding one pumpkinseed sunfish 30 *Helisoma trivolvis*. We measured diel oxygen flux in the mesocosms on the same day as the second *Physa* behavioral assay to measure relative net primary productivity across the nutrient treatments.

The effect of nutrient treatment on the predator avoidance index was tested using ANOVA, with pool row serving as a blocking factor. For *Physa*, the behavioral assay was performed twice, but the observations were not independent with respect to the nutrient enrichment effect, so the effect of nutrient treatments was analyzed using repeated measures ANOVA. Date of the behavioral assay was the repeated measure, and $n = 24$ for all analyses. Data were checked for normality and homogeneity, and log-transformed when necessary. We also calculated the 95% confidence interval of mean refuge use for each level of nutrient enrichment in order to evaluate whether refuge use was significantly different from zero.

Buffer study

In a laboratory study, we directly tested the effects of pH on the ability of snails to detect and respond to pumpkinseed sunfish. We cross-factored predation risk (predator cue or well water additions) with 6 pH levels ranging from 7.5 to 10.0 in 0.5-unit increments for each snail species, and each treatment combination was replicated six times, yielding 72 experimental units. pH was manipulated using carbonated water–sodium bicarbonate–sodium carbonate buffers. Snails were collected from local ponds and lakes and held in shaded pools with food for one week prior to the experiments. We conducted the experiment in polyethylene wash-tubs filled with 10 L of lake water. Buffers were added to establish the six pH treatments, and 10 snails were stocked into each tub. After snails acclimated for 48 hours, the pH of each tub was adjusted with additional buffers until it was within 0.2 pH units of the specified treatment. Predator cues were generated by feeding 30 snails to a single pumpkinseed sunfish housed in a 200-L mesocosm. After two hours, predator cue water (0.5 L) was transferred to each predator tub and 0.5 L of aged well water to each no predator tub. We added a ceramic tile to each tub to serve as a refuge and assessed snail habitat use once each hour for 3 hours following cue addition. We measured initial pH immediately after cue addition and again after the last set of behavioral observations. We present the arithmetic mean and 95% confidence interval of the actual hydrogen ion concentration for each pH and predator cue treatment combination because the actual pH did not exactly match target pH. The experiment was conducted twice, once using *Physa acuta* (mean shell length = 8.0 mm) and once using *Helisoma trivolvis* (mean shell length = 6.0 mm).

We took two complementary approaches towards analysis and description of the effect of predator cues and pH on anti-predator behavior. First, we used pH as a categorical variable and analyzed treatment effects with two-way ANOVA. The predator cue by pH interaction term tested the key hypothesis that the effect of predator cues on refuge use depended on pH. Additionally, we used non-linear regression to fit a logistic model to the relationship between predator avoidance and measured pH. Model parameters were used to estimate baseline avoidance values (effect of predator cues on refuge use at ambient pH) and threshold pH (pH at which avoidance decayed to one-half of the baseline value). Predator avoidance was calculated from the difference in refuge use between paired predator and no predator tubs. pH of paired tubs was always less than 0.1 pH unit different, and the mean

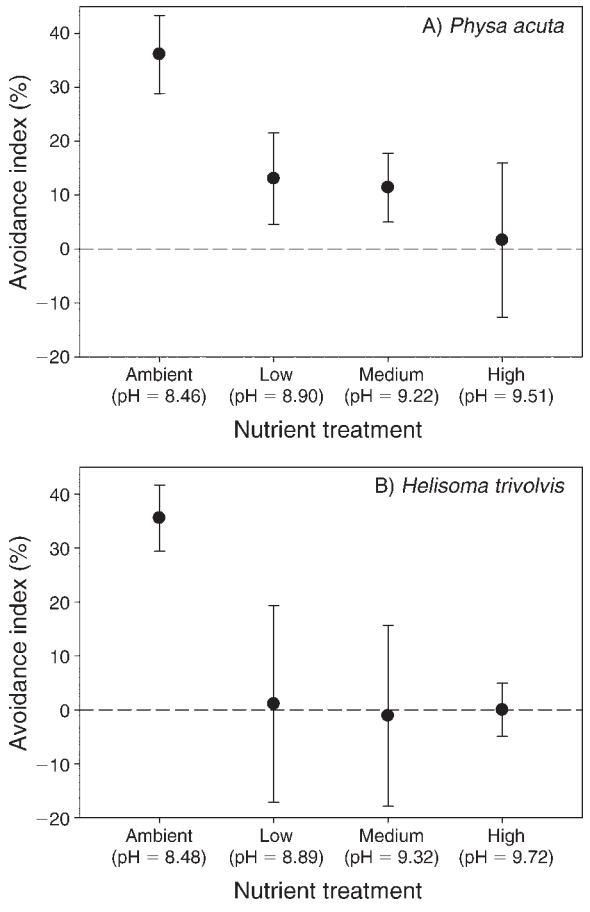

FIG. 1. Effect of nutrient additions on predator avoidance behavior by (A) *Physa acuta* and (B) *Helisoma trivolvis* in response to cues from pumpkinseed sunfish. Avoidance index is the mean difference in refuge use between paired predator and no predator tubs, and error bars represent 95% confidence intervals for the means ($n = 6$ observations at each nutrient level).

hydrogen ion concentration was calculated. Using the curve fitting algorithm in Sigmaplot 11.0 (Systat Software, San Jose, California, USA), we then fit the following model to the relationship between pH (x) and predator avoidance (y):

$$y = a \Big/ \left(1 + \exp[-(x - x_0)/b]\right)$$

where a represents the unimpaired, baseline avoidance, x_0 represents the threshold pH value at which avoidance falls to one-half the baseline value, and b is related to the slope of the decay of predator avoidance from the unimpaired baseline to zero.

RESULTS

Enrichment study

Nutrient enrichment had a large and significant effect on the magnitude of predator avoidance. Both snail species responded strongly to sunfish cues when housed in water drawn from unenriched mesocosms but showed no evidence of avoidance at the highest enrichment levels (Fig. 1). The avoidance index for *Physa* was 36% at ambient nutrient concentrations, declined to 13% and 11% at low and medium levels of nutrient enrichment, and was not significantly different from zero at the highest level of enrichment (nutrient effect on avoidance, $F_{3,19} = 15.5$, $P < 0.001$, model $R^2 = 0.72$). The *Physa* behavioral assay was performed twice, but there was no effect of date on refuge use ($F_{1,19} = 0.07$, $P > 0.10$) and no interactive effects of date and nutrients ($F_{3,19} = 1.55$, $P > 0.10$).

Similarly, *Helisoma* at ambient nutrients responded strongly to sunfish cues, with an avoidance index of 36% (Fig. 1). All three levels of nutrient enrichment impaired anti-predator behavior, with mean avoidance values not significantly different from zero (Fig. 1; nutrient effect on avoidance, $F_{3,19} = 18.9$, $P < 0.001$, model $R^2 = 0.78$). Primary productivity and pH increased in an ordinal manner with increasing nutrient loading (Appendix).

Buffer study

Both *Physa* and *Helisoma* responded to sunfish cues with increased refuge use, but the magnitude of the predator effect was dependent on pH as neither species responded to predator cues at the highest pH levels (Fig. 2). *Physa* responded strongly to predator cues in pH treatments 7.5 through 9.0, and the logistic model estimated a baseline difference in refuge use between predator cue and control tubs of 53%. Predator avoidance by *Physa* was weakened in pH treatment 9.5 and absent in pH treatment 10.0 (Fig. 2). The logistic model yielded a threshold pH of 9.4 for *Physa* (Fig. 3). ANOVA revealed significant effects of predator cue ($F_{1,60} = 265.1$, $P < 0.001$), pH ($F_{5,60} = 10.85$, $P < 0.001$), and the interaction of predator cue and pH ($F_{5,60} = 22.03$, $P < 0.001$; model $R^2 = 0.88$) on *Physa* refuge use.

Helisoma responded to sunfish cues with increased refuge use in pH treatments 7.5 through 8.5, with a baseline difference in refuge use between predator cue and control tubs of 33%. There was no significant effect of predator cues on *Helisoma* habitat use in pH treatments 9.0 through 10.0 (Fig. 2). The logistic model yielded a threshold pH of 8.8 for *Helisoma* (Fig. 3). Refuge use by *Helisoma* was affected by predator cue ($F_{1,60} = 38.41$, $P < 0.001$), pH ($F_{5,60} = 2.85$, $P = 0.02$), and the interaction of these two factors ($F_{5,60} = 5.17$, $P = 0.001$; $R^2 = 0.57$).

DISCUSSION

Organisms use odor plumes drifting through the environment to detect predators, recognize conspecifics and kin, locate mates, select habitats, and find food (Dodson et al. 1994, Dicke and Takken 2006, Derby and Sorensen 2008). Animals in aquatic environments are faced with the challenge of detecting small changes in the concentration of chemical cues associated with predators, food, or other relevant environmental fea-

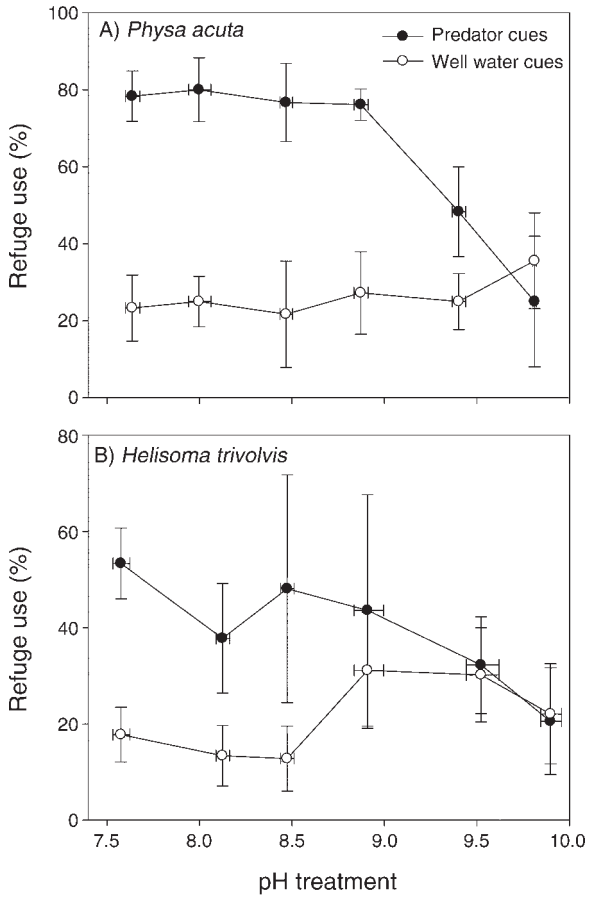

FIG. 2. Effect of pH on the anti-predator response of (A) *Physa acuta* and (B) *Helisoma trivolvis* to chemical cues from pumpkinseed sunfish as assessed in a laboratory study. Points represent mean refuge use at each pH level. Vertical and horizontal error bars represent the 95% confidence intervals for mean refuge use or hydrogen ion concentration.

tures, even though these cues are embedded within a complex olfactory background (Derby and Sorensen 2008). A small but growing number of studies have shown that alterations to the chemical environment can disrupt chemosensory perception. For example, elevated levels of heavy metals, pesticides, and surfactants have been shown to impair chemoreception in fish, snails, crustaceans, and amphibians (Blaxter and Hallers-Tjabbes 1992, Lefcort et al. 1999, Lurling and Scheffer 2007). Our results build on these studies by establishing that addition of a limiting nutrient can impair the chemosensory systems in an indirect manner by inducing a shift in pH. The effects of sensory impairment on survivorship and population growth may be profound because most aquatic organisms rely on chemoreception to cope with a complex and changing environment.

A large literature shows that animals cope with variable environments with shifts in behavior, morphology, life history, and physiology (Agrawal 2001, DeWitt and Scheiner 2004). Trait shifts require accurate information regarding the relevant environmental factors, as the costs for making a mistake can be substantial. Predator-induced trait shifts are known to have important community-level consequences, e.g., trait-mediated indirect effects (Turner and Mittelbach 1990, Peacor and Werner 2001). Thus, species are likely to interact by the flow of information from one individual to another (the information web) just as they interact by feeding relationships (the food web). We have focused here on detection of predators, but it is likely that chemosensory assessment of food, mates, and habitat choice will be similarly degraded. A disruption of feeding links can trigger changes in species abundances that cascade through the community (e.g., Paine 1966, Carpenter and Kitchell 1993). We predict that disruption of chemical information transfer will have similar cascading effects on community structure (see also Smee et al. 2008). This proposition, however, is difficult to evaluate at the moment, as environmental constraints on sensory perception have received little study, and the ecological consequences of sensory impairment have received no study.

Disruption of chemoreception could increase or lower mortality from predators, depending on whether pred-

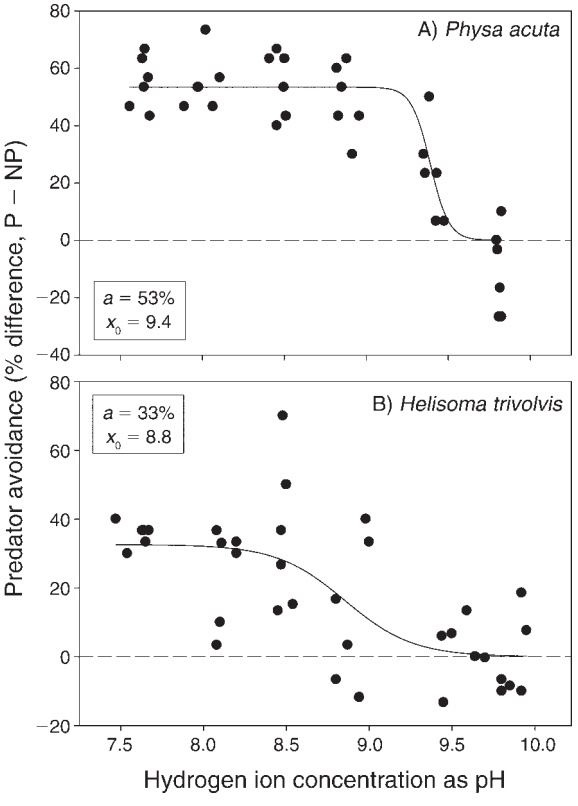

FIG. 3. Relationship between predator avoidance and pH as measured in a laboratory experiment. The parameter a represents the unimpaired, baseline avoidance, and x_0 is the threshold pH at which avoidance decays to one-half of the baseline value. Fitted logistic functions are highly significant, with model $R^2 = 0.80$ for *Physa* and 0.45 for *Helisoma*.

ator or prey suffers the greater sensory impairment, which in turn will depend in part on the sensory modalities employed by predator and prey (Smee and Weissburg 2006). In the case of pumpkinseeds and snails, pumpkinseeds are largely visual predators, so the likely effect of elevated pH will be to increase snail mortality rate. However, impairment of chemoreception could depress predator feeding rates and enhance survivorship of prey in systems with predators that rely heavily on chemosensory cues (e.g., crayfish).

The degree to which eutrophication actually impairs animal sensory capability in nature depends in part on the extent and frequency of high pH in aquatic systems. Our preliminary review of the evidence suggests that elevated pH is not an uncommon occurrence. Well known ecosystems with maximum pH values >9.0 include Florida Bay (Lapointe and Matzie 1996), Lake Apopka (Reddy and DeBusk 1991), and Chesapeake Bay (Serafy and Harrell 1993). O'Brien and deNoyelles (1975) report pH values as high as 11.0 in nutrient enriched ponds, and note that "there are numerous records of such high pH values in small lakes and ponds." Similarly, Hall et al. (1970) report pH values as high as 10.1 in experimentally fertilized ponds. There are technical challenges to obtaining accurate measurements of high pH values, but even given some scope for error, it appears that elevated pH occurs frequently, especially in anthropogenically eutrophied systems.

Elevated pH is caused by the intense photosynthesis stimulated by high nutrient loads, and the subsequent depletion of dissolved inorganic carbon. Even in systems with low carbonate availability, inorganic carbon is generally replenished by respiration, so depletion tends to be local and temporary (Talling 1976). Inorganic carbon depletion is expected to occur in surface waters if thermal stratification prevents mixing with deeper waters, or it may occur within dense beds of macrophytes if the macrophytes themselves inhibit mixing (e.g., Serafy and Harrell 1993). pH in productive systems will follow a diel pattern, peaking in mid-to-late day and falling at night (Maberly 1996). In sum, available data show that depletion of inorganic carbon and photosynthetically elevated pH occurs frequently but is a localized and episodic phenomenon.

There are several potential mechanisms by which elevated pH may impair chemoreception. Aquatic organisms use a complex suite of proteins, amino acids, amines, and other soluble, low molecular weight compounds to gather information from their environment (Weissburg et al. 2002, Derby and Sorensen 2008). Shifts in pH affect the charge of amino acids which can in turn lead to changes in protein structure and denaturation. Furthermore, these organisms have a wide variety of receptors that bind with a high degree of specificity to these compounds, and changes in pH can result in conformational changes in chemosensory receptors, leading to their inactivity (Wojtasek and Leal 1999).

Our results have important applied implications, as sensory impairment associated with elevated pH has not previously been reported, and thus is a newly discovered consequence of nutrient pollution. Eutrophication is the leading cause of water quality impairment in the United States and many other countries (Carpenter et al. 1998, Smith et al. 1998). Limiting both point source discharges and non-point loadings of P and N into surface waters is the goal of governmental initiatives at the local, state, and federal levels. Nevertheless, eutrophication continues to impair water quality across the United States and much of the rest of the world. The known consequences of eutrophication include hypoxia, blooms of blue-green algae, tainted drinking water supplies, and degradation of recreational opportunities (Smith et al. 1998). Our results extend the list of known consequences of eutrophication to include sensory impairment of aquatic animals, thereby drawing a direct link between the large-scale perturbation of biogeochemical cycles and the behavioral ecology of aquatic organisms. Given the widespread extent of water quality degradation associated with nutrient enrichment, chemosensory impairment as a result of eutrophication is likely a common occurrence in nature. More generally, efforts to establish ecologically relevant thresholds for pollutants of any sort should consider not only the short-term effects on survival and reproduction of individuals, but also longer-term consequences that account for perceptual impairment.

Acknowledgments

We thank Marty Heben, Drew Thompson, and Sharon Montgomery for assistance with experiments and the staff of the Pymatuning Laboratory of Ecology for logistical support. Kurt Regester, Suzie Boyden, and Alan Wilson provided helpful comments on the manuscript. This study was supported by a Sigma Xi Grant-in-Aid and by the National Science Foundation.

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APPENDIX

Effects of nutrient manipulations on primary productivity and pH (*Ecological Archives* A020-077-A1).