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Variable Background Flow on Aquatic Toxicant Exposure Alters Foraging Patterns on Crayfish

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Abstract

Climate change is expected to alter hydrological cycles on global and regional scales, impacting groundwater and surface water inputs to stream habitats. In the midwestern United States, the volume and frequency of inputs are expected to become increasingly variable. This region has a high incidence of agriculture, creating enormous potential for transport of pesticides and herbicides into aquatic ecosystems. Metolachlor, an herbicide for corn and soybean crops, has been demonstrated to contaminate surface water and groundwater in the region. This study examines the impact of variable flow conditions on the toxicity of environmentally relevant concentrations of metolachlor in a macroinvertebrate found in midwestern streams, the rusty crayfish (*Faxonius rusticus*). Changes in crayfish foraging behavior were analyzed using a Mixed Model ANCOVA. Under toxicant exposure, crayfish significantly increased their consumption of macrophytes, but only under the variable flow regime. Thus, the increased variability in toxicant exposure impacted crayfish foraging behavior more than other flow regimes. This significant interaction between flow regime and metolachlor exposure suggests that the greater variability in toxicant inputs to streams may lead to more severe changes in behavior for exposed organisms.

Keywords Dynamic exposure · Flow · Toxicity · Climate change · Runoff · Groundwater

The impact of anthropogenic contaminants spans both surface waters and groundwater reservoirs (Kreutzinger et al. 2004). Toxicants commonly enter the surface waters of rivers, lakes, and streams with wastewater effluent or are carried into these environments along with runoff (Amiard-Triquet et al. 2015). Wastewater effluent often contains substances such as pharmaceuticals and personal care products, many of which are endocrine disrupting compounds (Kreutzinger et al. 2004). Runoff, largely as a function of precipitation events and the surrounding terrestrial environment, can contain a wide variety of compounds, such as excess nutrients from fertilizer application, road salts, herbicides, and pesticides (Wang et al. 2017). Furthermore, many such contaminants are introduced into aquatic ecosystems indirectly via groundwater contamination. Groundwater enters a stream through the streambed, forming the baseflow of the stream (Bear and Cheng 2010). Toxicants from either surface water or soil can be introduced into groundwater reservoirs as water percolates through the soil (Reichenberger et al. 2007).

The introduction of contaminants into bodies of water is intimately tied to precipitation and the hydrological cycle. As such, factors influencing the rhythm of these natural cycles will also shape the nature of exposure events for aquatic organisms. Rising temperatures are anticipated to alter global hydrologic regimes substantially (Sedláček and Knutti 2014). Changes in the water cycle due to anthropogenic warming occur across a variety of factors: frequency and intensity of precipitation events, proportions of precipitation falling as rain and snow, evaporation, relative humidity, frequency of flooding events, and patterning of runoff (Nearing et al. 2004; Sedláček and Knutti 2014; Leng et al. 2016; Loecke et al. 2017). More

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than 40% of the United States is expected to experience significant changes in the variability of seasonal runoff inputs by the end of the century (Leng et al. 2016). In the twentieth century, the Great Lakes region of the midwestern U.S., a source of drinking water for upwards of 40 million people, has already seen an increase in the frequency of major storms and, consequently, in total precipitation (Patz et al. 2008). Heavy precipitation events are associated with the introduction of contaminants into the surface waters, with contamination events in the Great Lakes region typically occurring when daily rainfall surpasses approximately 5–6 cm (Patz et al. 2008). Furthermore, as temperatures rise, soil in the region is predicted to become drier during summer due to increased evaporation (Nearing et al. 2004). Concurrently, a higher proportion of precipitation is predicted to fall as rain instead of snow, leading to wetter winters. The culmination of drier summers and wetter winters, known as "climate whiplash", may increase the rate of percolation of water-soluble contaminants into groundwater reservoirs and local groundwater flow systems (Loecke et al. 2017). Approximately half of the streams in the Great Lakes region are fed primarily through groundwater (Grannemann et al. 2000). The introduction of toxicants through both runoff and groundwater contamination poses a considerable threat to Great Lakes region stream habitats. As climate change is likely to shape the frequency, intensity, and variability of these events, an understanding of changing hydrological cycles is critical to describing how contaminants move through stream ecosystems.

In streams, the spatial and temporal distribution of chemicals is dictated by flow (Denny 1993; Moore and Crimaldi 2004). At any given location in a stream, the concentration of a toxicant over time can be conceptualized as a series of pulses (Atema 1996; Edwards and Moore 2014). These intermittent pulses vary in their duration and magnitude as a function of turbulence, often reaching peak concentrations much greater than mean concentration (Edwards and Moore 2014). More laminar flow is associated with smoother, less dramatically fluctuating chemical peaks, hence more consistent exposure through time. Conversely, more turbulent flow is associated with patchier chemical plumes, giving rise to more intense fluctuations in exposure over time (Moore et al. 1992). Commonly, chemical toxicity is evaluated under static conditions (little or no flow). These testing conditions do not accurately reflect the dynamic exposure to chemicals that organisms will experience in natural stream environments. Fluctuation in chemical concentrations has repeatedly been demonstrated to influence the consequences of exposure for organisms, with more variable exposure often resulting in more negative outcomes (Milne et al. 2000; Ludington and Moore 2017; Neal and Moore 2017). Anticipating the likelihood of increasingly variable contamination events, the incorporation of fluctuation into exposure regimes is critical to appropriately evaluating toxicant impact on Great Lakes region streams in the context of climate change.

In addition to being a region of vital freshwater resources, the midwestern U.S. also produces nearly 80% of the nation's corn and soybean crops, creating opportunities for herbicides applied to agricultural fields to be transported into natural water bodies (Kalkhoff et al. 2003). One of many agricultural herbicides, metolachlor is a commonly used herbicide for corn and soybean crops across the United States. Due to its high water solubility and ubiquitous application, metolachlor percolates easily through soil and is often found in groundwater (Rivard 2003). In Ohio, while average annual stream concentrations of metolachlor are about 5 µg/L, these concentrations have been documented to intermittently rise to levels as high as 80 µg/L following rain events in the spring and summer (Frey 2001). Metolachlor concentrations generally rise with increased proximity to agricultural areas, with concentrations as high as 138 µg/L being documented in streams near agricultural fields (Rivard 2003).

The purpose of this study is to examine the impact of variable flow conditions on the toxicity of environmentally relevant concentrations of metolachlor in a macroinvertebrate commonly found in midwestern streams, the rusty crayfish (*Faxonius rusticus*). Crayfish are known to be sensitive to a variety of herbicides, such as metolachlor and atrazine (Wolf and Moore 2002; Cook and Moore 2008; Steele et al. 2018). Crayfish function as both predators and prey in stream ecosystems, as well as playing a vital, indirect role in food webs by breaking down terrestrial carbon inputs, creating food sources for other species (Hill and Lodge 1999). Discrepancies in the impact of metolachlor exposure under varying flow regimes may inform risk-assessment for herbicide introductions under increasing temperatures and shifting hydrological cycles.

Materials and Methods

This study utilized a 3×2 fully factorial design to assess the interaction between flow regime (three factors) and the consequences of metolachlor exposure (two factors) on the foraging behavior of the rusty crayfish (*F. rusticus*). Crayfish were exposed to metolachlor under three different stream flow regimes: low flow velocity (0.5 cm/s), high flow velocity (1.5 cm/s), and variable flow velocity (between 0.5 and 1.5 cm/s, see exposure arena section below). Control animals were exposed to the same flow regimes in the absence of metolachlor contamination, yielding a total of 6 treatments (below).

- Low Flow × Metolachlor Exposed (n = 9)
- Low Flow × Unexposed (n = 39)

- High Flow × Metolachlor Exposed (n = 9)
- High Flow × Unexposed (n = 25)
- Variable Flow × Metolachlor Exposed (n = 13)
- Variable Flow × Unexposed (n = 10)

After exposure to one of the three flow regimes in the presence/absence of metolachlor, foraging success of the crayfish was quantified for individual crayfish using a foraging assay (Wood et al. 2018).

Female, non-reproductive *F. rusticus* crayfish were hand collected from the Maple Bay of Burt Lake in Cheboygan County, MI (45.4873°N, 84.7065°W). Before exposure, animals were housed communally in a flow-through trough (237.5 × 86.4 × 60.1 cm: l × w × h) located at the University of Michigan Biological Station (UMBS) Stream Research Facility in Pellston, MI. Unfiltered water from the East Branch of the Maple River was pumped into the trough to maintain flow, allowing crayfish to feed on detritus contained in the water. Water temperature (approximately 19 °C) was not altered from ambient temperature upon entering the crayfish housing trough. Similarly, the housing trough was exposed to natural light: dark cycles (approximately 15:9 h), and these light:dark cycles were not manipulated during holding.

Only animals with all appendages intact were utilized in experimental trials. Before use in experimental trials, the right side of each crayfish's orbital carapace and right chelae were measured to allow for later analysis of possible size effects. Animals used in experimental trials had an average orbital carapace length of 2.3 ± 0.4 cm (SEM) and an average chelae length of 1.8 ± 0.2 cm (SEM).

Four artificial streams, to be used as exposure arenas, were constructed at the UMBS Stream Research Facility in Pellston, MI. Each stream (160 × 40.6 × 40.6 cm, interior L × W × H) was constructed from cinderblocks and lined with 4 mil plastic sheeting. The bottom of each stream was lined with a pea gravel substrate, which was maintained at a thickness of approximately 2.5 cm. To ensure that contaminated gravel and plastic from previous trials did not impact subsequent control trials, two streams were dedicated to control experiments and two streams were dedicated to exposure treatments.

Water was diverted from the East Brach of the Maple River and pumped into a constant head tank. Nylon mesh was placed over the inflow to the head tank to prevent large, particulate matter from accumulating and obstructing the head tank's outflow. Water flowed out of the head tank and into the exposure arenas via 1 cm (inner diameter) garden hosing, with an average output rate of 180 ± 5 mL/s per hose. Water exited artificial streams through outflow blocks at the downstream end of the exposure arena. These outflow blocks consisted of cinder blocks with openings obstructed by a wire mesh (0.14 × 0.16 cm mesh), allowing for control of the volume of water exiting the stream. The depth of water in each stream was held at approximately 22 cm and was held constant across all trials. To create distinct flow velocity treatments, low flow velocities utilized water inputs from only one hose, while high flow velocity treatments utilized inputs from three hoses. In variable flow treatments, irrigation timers (Melnor hydrologic four-zone timer) were used to alternate between inputs from one hose entering the stream and inputs from three hoses entering the stream. This resulted in the variable flow velocity stream alternating between low flow and high flow conditions at 3-h intervals. Thus, the variable treatment consisted of 3-h high flow followed by a 3-h low flow for 21 h and a single 1 h high flow period during the 22 h of exposure.

To allow for uniform toxicant introduction across all treatments, metolachlor was introduced into streams via a gravity feed system. Metolachlor or control solution was held in 22.7 L reservoir buckets at the upstream end of each exposure arena. Reservoir buckets were sealed with an opaque lid to prevent dilution in case of precipitation, introduction of contaminants, or photochemical reactions with the metolachlor solution. Solution flowed out of the reservoir buckets and into exposure arenas through 0.4 cm interior diameter aquarium tubing. The outflow of this tubing was buried below the stream's substrate. Consequently, solutions entered the stream by being fed upwards through the gravel, imitating groundwater introduction.

Both control and metolachlor solutions were introduced into streams at a constant rate of 0.44 mL/s. Environmentally relevant concentrations of metolachlor, 2 µg/L (low flow) and 2.1 µg/L (high flow) (measured at the location of the crayfish), were used throughout this experiment (Ludington and Moore 2017; Neal and Moore 2017). Metolachlor was 98.2% pure and purchased from Sigma-Aldrich. To ensure any variation in the patterning of exposure was a result of stream flow treatment, crayfish were tethered to a weighted tile at a consistent location in the exposure arena across all trials. For all exposure treatments, crayfish were located 20 cm downstream from the toxicant delivery system. Before exposure trials began, the dilution factor to this location in the stream was quantified using an EmStat3 + Blue electrochemical monitoring system (PalmSens, Houten, Netherlands). A dopamine-fluorescein tracer solution (0.113 g/L) was pumped into the stream via the previously described toxicant delivery system. Dopamine was certified reference standard grade and also purchased from Sigma-Aldrich.

The dilution factor for metolachlor within the artificial streams at the location of the animal was calculated using an EmStat3+ Blue electrochemical detection system (PalmSens, Houten, Netherlands). The EmStat system was fixed with a 30-µm carbon fiber electrode to measure oxidation–reduction reactions within the water column 5 cm about the gravel substrate (Edwards and Moore 2014; Harrigan and

Moore 2017; Ludington and Moore 2017). The chemical tracer, dopamine, was used in calculating the dilution factor as dopamine has an appropriate molecular weight for similar advective transport to that of metolachlor. The EmStat system sampled at the animal location 20 cm downstream of the chemical source at an interval of 20 Hz. The electrodes used were calibrated with known concentrations of dopamine prior to testing in the artificial streams. The stock solution of dopamine delivered to the artificial stream during EmStat recording was of the concentration 146.2 µM. A 47.7-fold dilution factor was calculated from the toxicant delivery system to the crayfish tether location under low flow velocity conditions. A 56.8-fold dilution factor was calculated from the toxicant delivery system to the crayfish tether location under high flow velocity conditions. These dilution factors were used to calculate the appropriate concentration for metolachlor stock solutions for each treatment. This process ensured animals across flow treatments were exposed to the same mean concentration of metolachlor, and toxicant exposure varied only in degree of fluctuation. Verification of concentrations of stock solutions of metolachlor were performed at the University of Michigan Analytical Chemistry Facility following the methods outlined in Yokley et al. (2002) using an LC–MS. Detection limits for metolachlor were orders of magnitude below the 2 ug/L being used in the streams.

Trials were run for a total of 22 h. Trials were run for 22 h to allow 2 h of rinsing between subsequent trials. Macrophyte samples (*Elodea canadensis*) were selected from their respective storage drums. All macrophytes were collected from Douglas Lake (Michigan) and only brightly colored and crisp textured plant samples were chosen for use in feeding trials. Approximately 1–1.5 g of the macrophyte was placed within a salad spinner (Farberware Basics, Item No. 5158683) to remove excess water before weighing to the nearest 0.001 g. After weighing, the plant stems were attached to glass rods (255 × 6 mm: l × OD) with 26-gauge green painted floral wire. After attaching plants to the rods, the rods were then placed within a hardware cloth brackets (24 × 19 cm: l × w) to hold the plant in place in the mesocosm. After the plant samples were placed into the mesocosms, a single animal was placed into the mesocosm. The crayfish's movement throughout the stream was limited by attaching a Velcro® piece to the carapace of each animal via superglue. The opposite Velcro® square was fastened to a tile weight using fishing line and placed in the stream to secure the animal's location to a particular area (Ludington and Moore 2017; Neal and Moore 2017). After addition of the crayfish, the toxicant was introduced into the stream. The following morning, all crayfish were removed first from the mesocosms. Once the crayfish were removed, the plant samples were removed from each mesocosm and were dried in the salad spinner again before weighing a second time.

Macrophyte biomass consumption (g) was calculated for the plants in each trial by subtracting the final mass of the plant samples after the trial from the initial masses of the plants before the trial. The resulting difference is the amount of macrophyte biomass that was either consumed or destroyed by the crayfishes' foraging activity. Changes in plant biomass were analyzed using a non-linear mixed model function (lmer) in R (R Core Team 2018; Bates et al. 2015). The plant biomass model was constructed with full interactions using toxicant presence (yes or no) and flow rate (high, low, variable) as fixed factors and a single random factor (mesocosm). When significant differences were found with the interaction terms, differential contrasts were used with a Tukey-HSD post hoc test in the emmeans function to determine where significant differences existed (R Core Team 2018; Lenth 2019).

Results and Discussion

All stock and dilution solutions used to prepare the metolachlor were within 5% of intended concentrations as verified by LC–MS. Based on these measurements stream concentrations remained within the expected averages of 2 µg/L ± 0.1 µg/L for the low, variable, and high flow. These were averages based on a volume of water (125 mL) collected over a 15 s period.

There was an overall interaction effect of macrophyte consumption based on the presence or absence of metolachlor and flow velocity ($F_{(2, 102, 0.05)} = 4.06$, $p = 0.02$). Post-hoc analysis showed significant differences in macrophyte consumption under variable flow and toxicant exposure compared to all other treatments ($p < 0.001$). Within this treatment, consumption of macrophyte material was three times the consumption in all other treatments (Fig. 1).

The results of this study demonstrate two findings regarding the consequences of metolachlor exposure for aquatic macroinvertebrates. Firstly, exposure to environmentally relevant concentrations of metolachlor can result in altered foraging behavior in the rusty crayfish (center Fig. 2). Alterations in percent macrophyte biomass consumption were observed between metolachlor-exposed animals and unexposed animals under variable flow treatments. Secondly, the consequences of metolachlor exposure for crayfish is dependent upon flow regime. While significant changes in macrophyte consumption were observed between exposed animals and control animals under variable flow, no such differences were observed between exposed animals and control animals under low flow or high flow treatments (Fig. 2). In fact, there were no significant differences between animals of any treatment, excepting animals exposed under variable flow conditions, which consumed a significantly

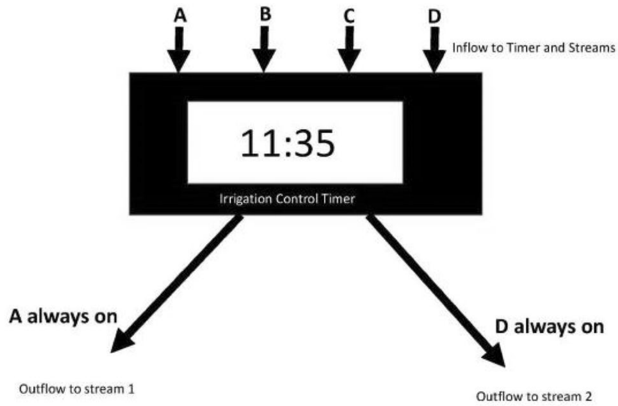

Fig. 1 Diagram of inflow and outflow of the irrigation control timer that created variable flow within the streams. Inflow line **a** was always flowing into stream 1 and Inflow line **b** was always flowing into stream 2. The irrigation control timer switched inflow lines **b** and **c** between the two streams at pre-defined times. This created a stream with either one or three inflow inputs

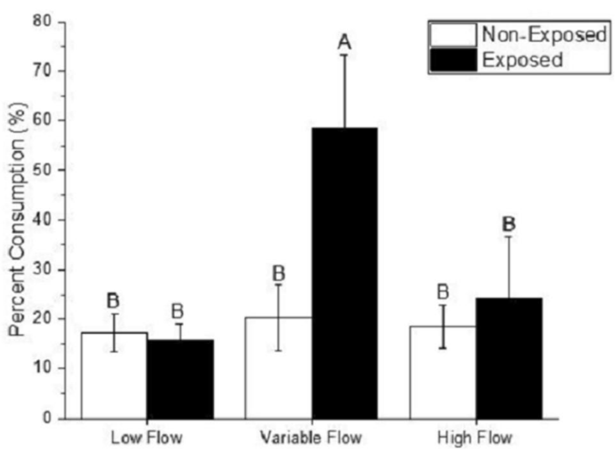

Fig. 2 Mean (±SEM) plant consumption for crayfish in exposure (black bars) and clean water treatments (white bars). Values are displayed for consumption under low flow (left hand), variable flow (middle), and high flow (right hand) treatments (flow speed in text of manuscript). Different capital letters indicate a significant difference using a linear mixed model followed by a Tukey-HSD post hoc analysis ($p < 0.05$)

higher percentage of available macrophyte biomass than all other treatments.

Previous work has demonstrated that static exposure to metolachlor impacts a number of important behavioral endpoints in crayfish, including aggression levels, anti-predator responses, and orientation toward food sources. Each of these behavioral endpoints contributes to the ability of crayfish to acquire food resources in natural environments. Crayfish exposed to metolachlor were significantly less aggressive in agonistic interactions with conspecifics (Cook and Moore 2008). For an exposed individual, this lessened aggression will likely translate into less dominant status within social hierarchies and resultantly diminished access to resources (Fero et al. 2007; Cook and Moore 2008). Metolachlor exposed crayfish have also been shown to demonstrate inappropriate responses to alarm-odors from injured conspecifics, often orienting towards the alarm cue (Wolf and Moore 2002). An inability to appropriately respond to these cues reduces the ability of the crayfish to successfully avoid predators, increasing the risk associated with time spent foraging. Lastly, previous work has established that metolachlor exposed crayfish are less successful in using chemical cues to orient toward food sources (Wolf and Moore 2002), which may result in less efficient foraging. Surprisingly, the results of this study indicate that variably exposed crayfish consumed a larger proportion of available plant biomass than their unexposed counterparts (Fig. 2). One possible explanation for increased consumption is compensation for increased nutritional needs to detoxify or repair tissue damage resulting from exposure. Exposure to atrazine results in increased expression of cytochrome P450, a detoxifying enzyme in the crayfish hepatopancreas, which may be an indicative of increased metabolic costs (Steele et al. 2018). Future investigation into the physiological impacts of herbicide exposure in crayfish may inform explanations of changes seen at a behavioral level. While the mechanism behind the observed increased plant consumption is unclear, any alteration in foraging patterns is likely to impact the fitness of metolachlor exposed animals, particularly in conjunction with other behavioral deficits.

In flowing environments, turbulent flow creates spatial and temporal heterogeneity in the distribution of chemicals. The degree of turbulent flow in a stream determines the patchiness of toxicant plumes as they move through the habitat (Denny 1993; Moore and Crimaldi 2004; Yee and Biltoft 2004). Additionally, the degree of turbulence will vary across locations within a stream as function of flow regime characteristics, such as flow velocity, interacting with physical stream characteristics, such as roughness of substrate (Nikora 2010; Edwards and Moore 2014; Harrigan and Moore 2017). Consequently, where toxicants enter the stream determines the degree of turbulence they will encounter (Steele et al. 2018). Chemicals introduced to a stream habitat through runoff contamination are likely to encounter greater turbulence, resulting in patchier plumes and more fluctuating exposure regimes. By contrast, chemicals introduced via groundwater contamination enter the stream in the boundary layer near the substrate, where flow is more laminar (Vogel 1994). This lesser degree of turbulence gives rise to more uniform exposure for benthic organisms, with less pronounced peaks in contaminant concentrations (Moore et al. 1994; Ludington and Moore 2017). Fluctuations in chemical concentration over time have been demonstrated to alter outcomes for exposed animals in both pulsed and dynamic exposure studies (Milne et al. 2000; Schultz and Liess 2000; Gordon et al. 2012). Often, dynamic exposure to a toxicant appears to result in more severely negative outcomes than static exposure of the same mean concentration (Neal and Moore 2017). This may be attributable to intermittent peak concentrations that are well above the average. Furthermore, the rapid onset and of chemical peaks associated with exposure in turbulent flow may not allow a sufficient window for recovery from previous chemical pulses. The relationship between toxicant peak characteristics and the consequences of exposure will be largely tied to the mode of uptake of the contaminant and the mechanism by which exposed animals are able to rid themselves of the substance (Ashauer et al. 2006; Neal and Moore 2017; Steele et al. 2018). In this study, the variability of flow tied to toxicant introduction may have created a temporally dynamic toxicant plume with greater concentration variation, which in turn contributed to the behavioral changes exhibited by animals in the variable flow treatment.

These results present serious considerations for exposure modeling in the context of climate change. While our results demonstrate that exposure to environmentally relevant concentrations of metolachlor can impact the behavior of benthic macroinvertebrates, these impacts were not apparent under steady flow conditions. As such, it is likely that traditional approaches to toxicity testing, such as static exposure testing, would be unable to capture the sensitivity of these organisms. More variable flow translates into more dramatically fluctuating, intermittent exposure for stream organisms (Ludington and Moore 2017). Depending on the organism and toxicant of interest, different toxicant pulse characteristics (e.g. maximum concentration, duration, intermittency between pulses) may have important implications for exposure outcomes (Edwards and Moore 2014; Ludington and Moore 2017). Consideration of the influence of flow in structuring toxicant pulses, and thereby behavioral and physiological outcomes, is a vital component of optimal toxicity tested and risk assessment.

As both local and global hydrological cycles shift because of climate change, the consideration of dynamic, variable exposure regimes becomes increasingly pertinent. The degree of turbulent flow in a given system has always shaped the movement of toxicants through stream environments. However, the drier summers and wetter winters anticipated as temperatures rise are likely to increase both the severity of contamination events and the magnitude of fluctuation in toxicant introductions throughout the year. As fluctuating exposure has been shown to result in more severe negative outcomes following exposure in certain systems (Neal and Moore 2017), it is possible that these shifting hydrological cycles will translate into increased sensitivity for aquatic organisms.

Exposure to sublethal concentration of metolachlor has repeatedly been demonstrated to impact crayfish behavior, specifically responses to alarm cues and foraging behaviors. Furthermore, the flow regime under which crayfish are exposed has been shown to impact behavioral endpoints. The next step in understanding how natural distributions of toxicants affect animals is to include larger scale variation in flow. This study took that step and demonstrated that variable flow is often associated with more pronounced behavioral impacts for organisms following exposure events. Climate change is anticipated to alter hydrodynamic cycles on both global and regional scales, in many cases resulting in more dramatically variable introduction of anthropogenic contaminants into natural bodies of water. As such, the incorporation of spatial and temporal variability is an essential consideration in evaluating toxicity in the context of a warming world.

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