The deal with diel: Temperature fluctuations, asymmetrical warming, and ubiquitous metals contaminants

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A B S T R A C T

Climate projections over the next century include disproportionately warmer nighttime temperatures ("asymmetrical warming"). Cool nighttime temperatures lower metabolic rates of aquatic ectotherms. In contaminated waters, areas with cool nights may provide thermal refugia from high rates of daytime contaminant uptake. We exposed Cope's gray tree frogs (Hyla chrysoscelis), southern leopard frogs (Lithobates sphenocephalus), and spotted salamanders (Ambystoma maculatum) to five concentrations of a mixture of cadmium, copper, and lead under three to four temperature regimes, representing asymmetrical warming. At concentrations with intermediate toxicosis at test termination (96 h), temperature effects on acute toxicity or escape distance were evident in all study species. Asymmetrical warming (day:night, 22:20 °C; 22:22 °C) doubled or tripled mortality relative to overall cooler temperatures (20:20 °C) or cool nights (22:18 °C). Escape distances were 40–70% shorter under asymmetrical warming. Results suggest potentially grave ecological impacts from unexpected toxicosis under climate change.

1. Introduction

Climate change is altering thermal patterns with potentially important repercussions for ectotherms simultaneously stressed by contaminants. Average global temperatures are projected to rise by 2.5–5.5 °C by 2099 (IPCC, 2014). Over most continental regions, including the United States, nighttime air temperatures are rising more quickly than daytime temperatures, resulting in reduced diurnal temperature ranges, so called "asymmetrical warming" (Li et al., 2012; IPCC, 2014). Nighttime air temperatures have increased by three to nearly seven times (Millett et al., 2009) faster than daytime temperatures over the past 50–100 years. Warming air temperatures appear to be driving current warming trends in freshwater ecosystems (Kausal et al., 2010). In general, average increases in air temperature of 2, 4, and 6 °C can cause freshwater systems to warm by 1.3, 2.6 and 3.8 °C, respectively (van Vliet et al., 2011). Models predict that warming in surface waters will follow the asymmetrical warming patterns of air temperatures with evidence of this already occurring in the San Francisco Estuary (Brooks et al., 2012).

Whether diel temperature fluctuations will stimulate or suppress physiological responses depends on the range of temperatures and where those temperature fluctuations fall within the thermal envelope of an ectotherm (Kingsolver et al., 2013). For example, when reared with diel temperature fluctuations from 32 to 18 °C the Australian marsh frog (Limnodynastes peronii) exhibited faster growth, shorter time to metamorphosis, and increased post-metamorphic jumping distance. Their performance was compared to controls reared under a constant temperature of 24 °C (Niehaus et al., 2006). In contrast, Arrighi et al. (2013) reported that developmental stage and tail length of Korean fire-bellied toad tadpoles (Bombina orientalis) increased in temperatures held steady at 20, 24, and 28 °C. Both metrics declined significantly when tadpoles were exposed to diel temperature fluctuations of 13 or 20 °C (Arrighi et al., 2013).

Warming temperatures and toxicants act as compounding stressors particularly for ectotherms. An impressive number of studies have investigated how increasing temperature can heighten the effects of toxicants (Heugens et al., 2001). Recently, this effect has been termed climate-induced toxicant sensitivity (CITS) based on the realization that when elevated temperatures increase the metabolic rates of aquatic ectotherms, animals increase their
respiration rates and food uptake to meet metabolic costs. Their increased contaminant uptake per unit time is greater than the key processes that mitigate toxicity—biotransformation and excretion—resulting in greater toxicity. On the other hand, toxicant-induced climate susceptibility (TICS) is the growing recognition that, independent of temperature, chronic contaminant exposure can also stimulate metabolism. Higher metabolism occurs because detoxification and elimination mechanisms must continually function at a higher rate. Chronically higher metabolism, from contaminants alone, occurs in fish (Beyers et al., 1999), larval amphibians (McDaniel et al., 2004), and bivalves (Lannig et al., 2008). Thus, researchers are raising the concern that organisms living in chronically polluted waters might be at greater risk from global warming if they cannot rally the additional energy needed to cope with compounding thermal stress (Lannig et al., 2008; Sokolova and Lannig, 2008; Hooper et al., 2013). Whether either the TICS or CITS hypothesis holds sway, cumulative stressors that increase risk in general (Landis et al., 2013) can divert energy resources from growth and reproduction; effects that can potentially cascade to impacts on populations and communities (Moe et al., 2013).

The worldwide distribution of sublethal contaminants makes their potentially cumulative effects important to wildlife conservation (Viers et al., 2009; Landers et al., 2010). Violations of the criteria that are protective of freshwater organisms, which are subject to site-specific exemptions, are not compiled nationwide (USEPA, 2009). Drinking water criteria, however, are monitored, and if appropriate, designated as legally impaired (i.e. 303(d) listed) under the United States Clean Water Act (United States Congress, 1972). Drinking water criteria have been set to allow for 10–100-fold less stringent than the criteria that apply to freshwater life. Over 42,000 individual waterways in the United States exceed drinking water criteria. Twenty-eight percent of these waterways are impaired because of metals contamination (USEPA, 2014). As discussed above, diel temperature fluctuations alone can have important impacts on biological responses (Caissie, 2006). To our knowledge, no studies examine the combined effects of asymmetrical warming and contaminant exposure. A few have examined the effects of contaminants when compounded by abrupt shifts from one acclimation temperature to another (Kimberly and Salice, 2014) and references therein. Moreover, laboratory studies conducted at constant mean temperatures are not always predictive of the results found under gradual diel temperature fluctuations (Niehaus et al., 2012). Herein we present the biological responses of aquatic organisms when asymmetric nighttime warming compounds effects of contaminants.

We investigated the effects of temperature regimes, which varied in level of diel temperature fluctuation, on the lethality and behavioral effects of metals mixtures in three amphibian species. We tested three hypotheses: 1) Nighttime cooling can provide significant thermal relief to aquatic ectotherms from effects of contaminated waters; 2) Nighttime temperatures and the effects of metals contaminants are significantly correlated; and 3) The response to elevated nighttime temperature is consistent among the distinct amphibian taxa tested herein.

2. Methods

2.1. Test Species

Cope’s gray tree frogs (Hyla chrysoscelis), southern leopard frogs (Lithobates sphenocephalus), and spotted salamanders (Ambystoma maculatum) were chosen to represent a variety of amphibian taxa whose ranges encompass extensive portions of the Eastern United States. According to the International Union for Conservation of Nature’s “Red List of Threatened Species”, all three species have widespread distributions and conservation ratings of “least concern” (www.iucnredlist.org). Adult Cope’s gray tree frogs have a critical thermal maximum (CTmax) of 38.0–41.5 °C (Blem et al., 1986; Lutterschmidt and Hutchison, 1997). Larval spotted salamanders have a CTmax of 28.1–37.9 °C (Keen and Schroeder, 1975). To our knowledge, the thermal sensitivity of southern leopard frogs has not been quantified. Larval southern leopard frogs, however, prefer temperatures of 17.5–30.4 °C, depending on their developmental stage (Dupre and Petranka, 1985), and larvae from the closely related northern leopard frog (Lithobates pipiens) have a CTmax above 37.0 °C (Noland and Gordon, 1981). We collected frog egg masses from ponds at Southern Illinois University and salamander eggs in the Shawnee National Forest, Illinois.

2.2. Experimental design

We ran toxicity tests with a full factorial experimental design of three replicates, five metals treatments, and three or four temperature regimes for salamander and frog species, respectively. Test duration was 96 h. This full factorial type of research design consists of experimental treatments from all combinations of the levels of two or more distinct treatment factors. For example, this study was a 5 × 3 or 5 × 4 factorial arrangement, meaning all five levels of metals appear in combination with all 3 or 4 temperature regimes. Temperature regimes varied by day:night temperatures, representing a range of diel temperature variation, meant to encompass possible effects of asymmetrical nighttime warming (Fig. 1). The test matrix consisted of filtered (1.0 µm ashed, glass fiber filters) lake water plus four additions of a metals mixture of Cd, Cu, and Pb, for a total of five treatments (Table 1). Upon hatch, five larval salamanders or ten larval frogs were placed in 800 ml tri-pore beakers with 600 ml of test matrix per replicate. Beaker locations were randomized within incubators (Thermo incubators, model 818). All tests ran for 96 h with 14:10 day–night light cycles. Temperatures were adjusted by 0.5 °C every half hour after a change in light until daytime or nighttime test temperature was reached. Test solutions were renewed daily. During renewals, dead larvae were counted, and dead larvae were removed.

Temperature treatments had nominal targets of 22:22, 22:20, and 22:18 °C for all species. For Cope’s gray tree frogs and southern leopard frogs, we added a constant temperature regime of 20:20 °C (Fig 1). These temperature regimes are biologically conservative because temperatures are well below the CTmax or within the preferred temperature range of all three species, particularly the larval southern leopard frog (see section 2.1. Test Species, above).

Fig. 1. (Single column image) Average temperatures in bioassays. Target values for temperature regimes are listed as day:night. The 20:20 treatment was not present in the spotted salamander experiments.
Moreover, chosen temperature regimes fall well within the range of temperatures in natural breeding ponds of all study species. Finally, temperature regimes were chosen to represent a hypothetical gradient of nighttime temperatures that fall within the 2.5–5.5 °C range of projected temperature shifts over the next century due to global warming. The constant 20:20 treatment was added to better our understanding of the effects of temperature variability itself (i.e. there may be differences in percent mortality between the 22:18 and 20:20 treatments even if their mean temperatures are similar). Throughout the tests, we recorded the temperature every 15 min within each temperature treatment, with a temperature data logger placed in separate tri-pore beaker that contained the same 600 ml volume of test matrix.

Every 24 h we measured the instantaneous temperature, dissolved oxygen, and conductivity of a random replicate of each concentration in each temperature. We measured ammonia, alkalinity, and hardness of a random replicate of each concentration in each temperature. We measured ammonia, alkalinity, and hardness of a random replicate of each concentration in each temperature. At the beginning and end of the 96-h exposures, we analyzed test waters for dissolved anions (F, Cl, NO3, NO2, SO4, PO4; by ion chromatography; ICS-2100, Dionex) and dissolved organic carbon (DOC; by catalytic combustion; TOC-VCSN, Shimadzu). Test metals (Cd, Cu, and Pb) were analyzed by graphite furnace atomic absorption (Ca, K, Mg, Na; AA240FS, Varian). All metals treatments are presented as bioavailable chronic criterion units (BCCUs), total concentrations, and BCCU values for each metal. BDL – below detection limit.

<table>
<thead>
<tr>
<th>Treatments (sum BCCUs) Avg (±SE) (µg L⁻¹)</th>
<th>Metal</th>
<th>Total Avg (±SE)</th>
<th>BCCU Avg (±SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 (1)</td>
<td>Cd</td>
<td>BDL</td>
<td>BDL</td>
</tr>
<tr>
<td></td>
<td>Cu</td>
<td>0.7 (0.2)</td>
<td>3.1 (0.8)</td>
</tr>
<tr>
<td></td>
<td>Pb</td>
<td>BDL</td>
<td>BDL</td>
</tr>
<tr>
<td>53 (2)</td>
<td>Cd</td>
<td>23.6 (1.7)</td>
<td>18.6 (1.3)</td>
</tr>
<tr>
<td></td>
<td>Cu</td>
<td>5.5 (0.8)</td>
<td>22.6 (3.1)</td>
</tr>
<tr>
<td></td>
<td>Pb</td>
<td>0.1 (0.1)</td>
<td>11.8 (1.5)</td>
</tr>
<tr>
<td>80 (3)</td>
<td>Cd</td>
<td>38.2 (2.6)</td>
<td>30.2 (2.1)</td>
</tr>
<tr>
<td></td>
<td>Cu</td>
<td>8.0 (1.4)</td>
<td>33.0 (5.7)</td>
</tr>
<tr>
<td></td>
<td>Pb</td>
<td>0.2 (0.1)</td>
<td>17.2 (2.6)</td>
</tr>
<tr>
<td>101 (6)</td>
<td>Cd</td>
<td>49.5 (3.4)</td>
<td>37.1 (2.7)</td>
</tr>
<tr>
<td></td>
<td>Cu</td>
<td>10.9 (2.1)</td>
<td>38.3 (8.8)</td>
</tr>
<tr>
<td></td>
<td>Pb</td>
<td>0.2 (0.1)</td>
<td>25.2 (5.6)</td>
</tr>
<tr>
<td>140 (8)</td>
<td>Cd</td>
<td>67.6 (2.8)</td>
<td>51.3 (2.2)</td>
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<tr>
<td></td>
<td>Cu</td>
<td>13.7 (2.7)</td>
<td>47.8 (11.2)</td>
</tr>
<tr>
<td></td>
<td>Pb</td>
<td>0.4 (0.1)</td>
<td>41.3 (9.4)</td>
</tr>
</tbody>
</table>

2.3. Statistical analysis

We used analysis of variance (ANOVA) to test for differences in mortality among temperature treatments. Significantly lower mortality in temperature treatments with lower nighttime temperatures would indicate the benefit of thermal refugia (hypothesis 1). To add predictive power to our analyses, and to tease apart the effects of nighttime temperatures from daytime temperatures, we used multiple regression analyses of percent mortality at test termination on mean daily minimum and maximum temperatures. At low concentrations, contaminants had little or no effect on survival, whereas, at high concentrations, contaminants caused intermediate to 100% mortality. Multiple regression analyses were conducted on concentrations with intermediate toxicosis at contaminant levels that were appropriate for the specific toxicant sensitivity of each species (hypothesis 2). For the explanatory temperature data, we used the mean daily minimum and maximum temperature values from data loggers in each temperature regime. Since we were primarily interested in the effects of nighttime temperature on percent mortality, we used multiple regression to separate the significant effects of the two extremes in mean daily temperature. Significantly lower mortality in treatments with lower nighttime temperature indicates the benefit of thermal refugia in contaminated waters. Furthermore, any significant relationship between mean daily minimum nighttime temperature and percent mortality indicates that continued asymmetrical warming of nighttime temperature may remove thermal relief that currently exists (hypothesis 2).

Although often complex, behavioral responses to environmental factors may show effects when simple mortality does not. We therefore used ANOVA to test the effect of nighttime temperature on our one behavioral endpoint: maximum escape distance. When ANOVA results were significant, we used Tukey HSD tests to examine pairwise differences between temperature treatments. To avoid pseudoreplication, the distances of all individuals tested from within a single test beaker were averaged. Beaker averages were used as the statistical unit for the above analyses. Significant ANOVA findings would indicate an effect of temperature treatment on maximum escape distance (hypothesis 1). Both ANOVA and
3. Results

Effect concentrations causing mortality at 96 h varied among species (Fig. 2). Spotted salamanders were approximately as resistant to metals toxicity as southern leopard frogs; both of which had almost 100% survival in exposures less than 101 BCCU. In contrast, some Cope’s gray tree frogs died even at the baseline dose. Temperature regimes had little apparent effect on mortality at metals doses far below the animal’s toxic threshold (e.g. 100% survival at doses less than 101 BCCU for spotted salamanders and leopard frogs) or at doses that greatly exceeded their tolerance for metals (e.g. zero survival of Cope’s gray tree frogs at doses greater than 80 BCCUs).

At concentrations with intermediate toxicosis after 96 h, significant differences in mortality among temperature regimes supported hypothesis 1 in two out of three of our study species. In Cope’s gray tree frogs, the temperature regimes with the lowest nighttime temperature (22:18) and constant low temperature (20:20) had significantly lower mortality than the treatment with the highest nighttime temperature (22:22). In southern leopard frogs, at 101 BCCU, the temperature regime with the second lowest nighttime temperature (22:20) had significantly lower mortality than the temperature regime with the highest nighttime temperature (22:22). At this concentration, the constant lower temperature regime (20:20) had significantly lower mortality than all other temperature regimes, indicating potential sensitivity of southern leopard frogs to diel temperature fluctuations. At 140 BCCU, southern leopard frogs in the lowest nighttime temperature regime had significantly lower mortality than the second highest nighttime temperature regime (22:20), but neither could be compared to the temperature regime with the highest nighttime temperature (22:22) due to complete mortality in that treatment.

Results of multiple regression analysis on treatments with intermediate mortality supported our second hypothesis that mean daily minimum and maximum temperatures significantly correlated with mortality in two of our three study species. At 4 and 53 BCCU, increases in mean daily minimum temperature significantly increased the percent mortality of Cope’s gray tree frogs (Table 2). At 101 BCCU, increases in mean daily minimum temperature increased mortality in southern leopard frogs. At 140 BCCU, regression analysis was not significant but the trend for southern leopard frogs remained the same. There was no significant effect of mean daily minimum temperature on mortality for spotted salamanders.

Significant effects of nighttime temperature on the maximum escape distances in two of the three species also supported hypothesis 1 (Table 3). For spotted salamanders, the average escape distance in 101 BCCU exposures was significantly different at each temperature from all others (Tukey HSD, all p-values < 0.01). Furthermore, the highest nighttime temperature had the shortest average escape distance, which was 68% below the distance moved by salamanders in the lowest nighttime temperature. There was a significant effect of temperature on the maximum escape distance of southern leopard frogs at 80 BCCU. At this concentration, the average escape distance at the warmest nighttime treatment was 70% shorter than all other temperature regimes. Thus, our third hypothesis was supported by observations that all three species benefited from lower nighttime temperatures in relation to significantly lower mortality or significantly greater escape distances.

4. Discussion

We examined how three amphibian ectotherms respond to the compounding stresses of metals pollution coupled with asymmetrical warming. We postulated that organisms coping simultaneously with both chronic thermal stress and contaminant stress would exhibit greater thermal sensitivity at the same life stage. This general prediction was based on an earlier study in which we observed that growth of Cope’s gray tree frog was unaffected when exposed to increases of +1.5 and +2.5 °C with diel cycles until exposed to elevated levels of contaminants (Hallman and Brooks, in review). This finding indicated susceptibility to changes in climate depending upon contaminant levels (i.e. TICS).

Separating the effects of multiple stressors is often a question of, “Which came first, the chicken or the egg?” We expected our results to support the TICS hypothesis of greater toxicant-induced climatic (i.e. thermal) sensitivity. Our findings, however, do not confirm either the TICS or CITS hypothesis alone. Our results demonstrate that in contaminated waters causing intermediate
Table 2
Results of multiple regression analyses for percent mortality versus mean daily minimum temperature (MinTemp) and mean daily maximum temperature (MaxTemp) for two focal species in mixtures of Cd, Cu, and Pb. BCCU = bioavailable chronic criterion unit. While not significant at α = 0.05, the last regression follows the trend for intermediate mortality.* indicates significant value. For spotted salamanders with intermediate mortality, no regression analyses were significant (p-values <0.79) and those analyses explained no more than 7% of the variation in mortality (R² ≤ 0.07).

| Temp regime | Coefficients | Estimate | Error | t value | Pr(>|t|) | R² | p-value |
|-------------|--------------|----------|-------|---------|----------|-----|---------|
| **Spotted salamanders** | Intercept | -0.609 | 0.383 | -1.590 | 0.146 | 0.490 | 0.048* |
| | MinTemp | 0.041 | 0.014 | 2.906 | 0.017* | 0.490 | 0.048* |
| | MaxTemp | -0.005 | 0.016 | -0.295 | 0.774 | 0.595 | 0.171* |
| **Southern leopard frog** | Intercept | -2.360 | 0.781 | -3.021 | 0.014* | 0.595 | 0.171* |
| | MinTemp | 0.068 | 0.029 | 2.386 | 0.041* | 0.595 | 0.171* |
| | MaxTemp | 0.067 | 0.033 | 2.046 | 0.071 | 0.595 | 0.171* |

Table 3
Differences in behavioral responses among temperature treatments at 96 h of exposure to metals mixtures at 101 BCCU for spotted salamanders and 80 BCCU for leopard frogs. For Cope’s gray tree frog at 96 h, behavior did not differ significantly among any temperatures within any metals concentration level. BCCU = bioavailable chronic criterion unit. Temp regime = day:night water temperatures (°C). Different superscripts indicate significant differences among temperature regimes. n.a. = not applicable. Distances are in cm.

<table>
<thead>
<tr>
<th>Temperature regimes</th>
<th>Spotted salamanders</th>
<th>Southern leopard frog</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean escape distance (SD)</td>
<td>11.51 (2.12)*</td>
<td>11.94 (3.13)*</td>
</tr>
</tbody>
</table>

4.1. Potential mechanisms for impaired survival and escape behavior

Ultimately, organisms are energy limited. As limits are approached, both thermal sensitivity and contaminant sensitivity spiral upward, potentially to a fatal tipping point (Sokolova, 2013). Observed responses to compounding stressors are consistent with the concept of a dynamic energy budget (Nisbet et al., 2000; Vazeur et al., 2014). Within the bounds of an organism’s dynamic energy budget, each compounding stressor imposes a physiological cost. Organisms can cope effectively with any combination of energy demands so long as total demands do not exceed their maximal energy limit (Sokolova, 2013). If energy stores are adequate, organisms maintain a positive energy balance that supports not only survival, but also the additional resources necessary to grow and reproduce (Nisbet et al., 2010). Under global warming, ectotherms are particularly at risk. As rising temperatures increase metabolism, energy demands build. Increased demands can compound existing stressors, such that ectotherms cannot tolerate warmer water (Portner et al., 2010).

Several mechanisms of metals exposure potentially contribute to the compounding effects of warming temperatures observed herein. Chronic exposure to metals alone can elevate basal metabolic rate independently of temperature, because metals increase energy demands for cellular detoxification and repair (Calow, 1991). Greater maintenance costs stem from production of compounds that detoxify metals — metallothionein (Cooper and Fortin, 2010) and glutathione (Sura et al., 2006). Ultimately, higher metabolic costs can limit energy for coping with heat stress. For example, cadmium can directly inhibit production of heat shock protein 70 (HSP 70) in clam and oyster hemocytes (Ivanina et al., 2014). Whether lower HSP 70 translates into greater temperature sensitivity in bivalves was untested.

Aside from greater energy demands that might limit thermo-regulation, metals can decrease the overall energy that an organism has available to deal with compounding environmental stressors. Metals can decrease oxygen transport by lowering hemoglobin levels (Arrieta et al., 2000; Vinodhini and Narayanan, 2009) and interfere with cellular energy production in mitochondria (Sokolova and Lannig, 2008). Warmer waters contain less oxygen so that the fundamental niche of animals challenged by contaminants must be cool, higher-oxygen waters (Portner et al., 2010).
Regardless of the mechanism, pronounced responses to relatively small changes in nocturnal temperatures that we observed indicate potentially important ecological repercussions.

4.2. Ecological implications

Due to inter-specific distinctions in the chemical and thermal tolerances of aquatic organisms, the ecological implications of asymmetrical warming and contaminants as compounding stressors are difficult to predict. To our knowledge, no other studies have examined the compounding effects of asymmetrical warming and contaminant exposure, thus, clear trends in aquatic ectotherms cannot be defined.

Nonetheless, general patterns of physiological response to diel temperature fluctuations alone are emerging with interesting ecological implications. Immune function and growth appear to benefit from nighttime cooling so long as diel temperature fluctuations are gradual and fall within typical ranges of daily temperatures. For example, hellbenders (Cryptobranchus alleganiensis) subjected to natural patterns of diel temperature fluctuations in gradual half hour increments from 16 to 26 °C showed enhanced innate immune function (blood kill assays) compared to stable, but warm temperatures (21 °C) (Terrell et al., 2013). Striped marsh frogs exhibited greater jumping performance, greater size, and faster metamorphosis under treatments with diel temperature fluctuations from 18 to 32 °C than under treatments with a constant temperature of 25 °C (Niehaus et al., 2006).

In contrast, abrupt thermal shifts, or warm, constant temperatures without thermal relief may lower immune competence and result in smaller size at maturity. Cuban tree frogs (Osteopilus septentrionalis) subjected to abrupt diel fluctuations from 15 to 25 °C exhibited lower immune competence (Raffel et al., 2013), and striped marsh frog tadpoles reared under diel fluctuations of 14–34 °C were smaller than those reared in treatments with diel fluctuation of 22–26 °C or constant temperatures (Niehaus et al., 2011).

4.3. Implications for conservation

Independent of the effects of contaminants, aquatic organisms often seek low temperature habitats to avoid thermal stress (Schaefer et al., 2003). If air temperatures rise by 2.5 °C by 2099, as predicted by the IPCC, then water temperatures will likely rise by a similar extent. If, as expected, water temperatures follow the asymmetrical warming patterns of air temperatures, then the majority of these increases will be in nighttime temperature. In contaminated freshwater systems, thermal refugia in deep pools or riffles may prove critically important to organisms to avoid excessively high uptake rates. Such local refugia may allow organisms to survive in waters that would be unsuitable at constant, elevated temperatures. At a larger scale, regions with greater diel temperature fluctuations may serve as refugia for species whose ranges are greatly affected by asymmetrical warming. As nighttime temperatures increase due to asymmetrical warming, these large-scale refugia may disappear at a faster rate than would be detected by examining average temperature alone. As refugia are lost, stricter regulations on contaminant loads may be required to aid in conservation.

Wild terrestrial and aquatic populations are declining worldwide (Dirzo et al., 2014). Moreover, population declines are observed in aquatic habitats despite improvements in flow and mitigation of point-source pollution (Brooks et al., 2012). Across habitats, climate change compounds existing sublethal stressors. More research is necessary to develop predictive models of the effects of multiple stressors. Although our results warn of potential impacts of asymmetrical warming, this study is just the first step. Waters contaminated with sublethal cocktails of contaminants have become the new norm (Viers et al., 2009; Landers et al., 2010). Chronic toxicity tests under temperature regimes of asymmetrical warming are required to understand the impacts that contaminants have on temperature sensitivity. Given that laboratory studies at constant mean temperatures may not be predictive of responses under diel temperature fluctuations (Niehaus et al., 2012), instead of representing projected changes in temperature as increasing plateaus of constant temperatures, studies of compounding stressors will benefit by including diel temperature fluctuations and the asymmetry associated with projected warming. Future research is needed on both the mechanisms of thermal relief in the laboratory and the ecological roles of thermal refugia in the wild.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.envpol.2015.06.005.

References


