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Integrating both interaction pathways between warming and pesticide exposure on upper thermal tolerance in high- and low-latitude populations of an aquatic insect☆

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ABSTRACT

Global warming and chemical pollution are key anthropogenic stressors with the potential to interact. While warming can change the impact of pollutants and pollutants can change the sensitivity to warming, both interaction pathways have never been integrated in a single experiment. Therefore, we tested the effects of warming and multiple pesticide pulses (allowing accumulation) of chlorpyrifos on upper thermal tolerance (CTmax) and associated physiological traits related to aerobic/anaerobic energy production in the damselfly *Ischnura elegans*. To also assess the role of latitude-specific thermal adaptation in shaping the impact of warming and pesticide exposure on thermal tolerance, we exposed larvae from replicated high- and low-latitude populations to the pesticide in a common garden rearing experiment at 20 and 24 °C, the mean summer water temperatures at high and low latitudes. As expected, exposure to chlorpyrifos resulted in a lower CTmax. Yet, this pesticide effect on CTmax was lower at 24 °C compared to 20 °C because of a lower accumulation of chlorpyrifos in the medium at 24 °C. The effects on CTmax could partly be explained by reduction of the aerobic scope. Given that these effects did not differ between latitudes, gradual thermal evolution is not expected to counteract the negative effect of the pesticide on thermal tolerance. By for the first time integrating both interaction pathways we were not only able to provide support for both of them, but more importantly demonstrate that they can directly affect each other. Indeed, the warming-induced reduction in pesticide impact generated a lower pesticide-induced climate change sensitivity (in terms of decreased upper thermal tolerance). Our results indicate that, assuming no increase in pesticide input, global warming might reduce the negative effect of multiple pulse exposures to pesticides on sensitivity to elevated temperatures.

1. Introduction

Global warming and chemical pollution are two major threats to ecosystems (Brönmark and Hansson, 2002; Millenium Ecosystem Assessment, 2005) that have the potential to interact. On the one hand, many studies demonstrated that warming can alter the toxicity of pollutants (Noyes et al., 2009; Holmstrup et al., 2010; Moe et al., 2013; Noyes and Lema, 2015), called climate-induced toxicant sensitivity (Hooper et al., 2013). On the other hand, and less studied, pollutants are able to impair an organism's ability to cope with increased temperatures (toxicant-induced climate change sensitivity; Sokolova and Lannig, 2008; Hooper et al., 2013; Moe et al., 2013; Noyes and Lema, 2015). The existence of both interaction pathways indicates the inherent complexity in understanding and predicting the effects of global warming and toxicant exposure in a changing world. So far both interaction pathways have not been integrated in a single experimental study. Moreover, the strength of each interaction pathway can have a strong geographic signal and differ between populations of the same species living in different thermal conditions (Dinh Van et al., 2013; Noyes and Lema, 2015).

The increased toxicity of many pollutants at higher temperatures may not necessarily translate into a higher negative impact on organisms. Indeed, exposure to pollutants such as pesticides may decrease at higher temperatures because of higher degradation rates in the medium (Hooper et al., 2013). Under multiple pulse scenarios where pollutants such as pesticides can accumulate

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(Reinert et al., 2002), these effects of different degradation rates will likely influence the exposure to pesticides (assuming no increase in pesticide input, but see Kattwinkel et al., 2011). These global warming related changes in toxicant exposure can result in climate-induced toxicant sensitivity as explicitly considered in recent reviews (Fig. 1 in Moe et al., 2013; and Fig. 1 in Noyes and Lema, 2015). As this interaction pathway is through changed exposure and not just through changed toxicity of a pollutant at a given concentration (which likely occurs simultaneously), we will more generally call this interaction pathway "climate-induced toxicant impact" to indicate it addresses the net impact of climate-induced changes in exposure and sensitivity. Further, due to thermal evolution populations in warmer, low-latitude regions may have a higher energy budget at higher temperatures (Stoks et al., 2012), and as a result suffer less from increased toxicity under warming (Dinh Van et al., 2013). While multiple-pulse scenarios and thermal evolution likely also shape how pollutants affect upper thermal tolerance, this has not been studied. Yet, understanding effects on thermal tolerance is of paramount importance to understand how populations will be able to deal with warming in a polluted world (Huey et al., 2012).

Increased energy demand for maintenance of basal metabolism that is not met by increased generation of energy is central to the stress effects caused by temperature and pollutants, and therefore a likely physiological mechanism underlying how pollutants may shape thermal tolerance (Sokolova and Lannig, 2008; Noyes and Lema, 2015). Given the central role of oxygen in aerobic metabolism, oxygen may become limiting near upper limits of thermal tolerance (CTmax) due to a mismatch between increased oxygen demand and limited supply capacity to deliver oxygen to the tissues/organs (Pörtner et al., 2006; Pörtner, 2010; Verberk and Bilton, 2011). This will reduce the aerobic scope, the excess capacity to deliver oxygen (Verberk et al., 2016). Near thermal maxima this limitation in aerobic scope will lead to a transition to anaerobic metabolism after which survival becomes passive and time-limited (Pörtner and Knust, 2007; Verberk et al., 2016). As also pollutants can strongly impair aerobic capacities and impose an elevated energy demand for basal metabolism (Calow, 1991; Beyers et al., 1999), it is thought that the combination of warming and pollutants will result in an earlier onset of aerobic energy deficiency, thereby lowering the upper thermal tolerance (Sokolova and Lannig, 2008). For example, in eastern oysters *Crassostrea virginica*, exposure to cadmium lowered the upper critical temperature and this was associated with a decrease of the aerobic scope and an early transition to partial anaerobiosis (Bagwe et al., 2015).

The main objective of this study was to test how warming and multiple pulses of the pesticide chlorpyrifos jointly shape upper thermal tolerance in larvae of the damselfly *Ischnura elegans*. By exposing larvae to the pesticide at different temperatures and afterwards look at effects on thermal tolerance we can provide an integrated test of both interaction pathways between warming and pesticide exposure. Chlorpyrifos (CPF), an organophosphorus compound, is one of the most frequently used pesticides worldwide (Eaton et al., 2008), and is a priority pollutant in the Water Framework Directive (2000/60/EC). We applied the pesticide in multiple pulses without renewal of the medium; this allows different degradation rates at different temperatures leading to temperature-dependent accumulation of CPF in the water. This reflects a more realistic exposure scenario than exposure under static concentrations. Damselfly larvae are important intermediate predators in aquatic food webs and are particularly vulnerable to global warming (Hassall and Thompson, 2008) and organic pollutants (Liess and Von der Ohe, 2005). Furthermore, they have proven elegant study organisms to address ecological and evolutionary questions in ecotoxicology (Stoks et al., 2015). To be able to detect local thermal adaptation we performed a common garden warming experiment in which larvae originating from replicated high- and low-latitude populations in Europe were reared from the egg stage at 20 and 24 °C, the mean summer water temperature at high and low latitudes, respectively (De Block et al., 2013). The 4 °C temperature difference matches the predicted warming at the high latitude under IPCC (2013) scenario RCP8.5. As measure of upper thermal tolerance we determined the critical thermal maximum (CTmax), the temperature were animals no longer show body movements or muscular spasms (Verberk and Bilton, 2013). To explore physiological mechanisms associated with effects on CTmax, we quantified the activities of two enzymes related to aerobic/anaerobic energy production, pyruvate kinase (PK) and lactate dehydrogenase (LDH), and the amount of lactate as anaerobic metabolite. We predicted that the negative impact of multiple pulse exposure to CPF on thermal tolerance (and associated changes in physiological traits indicating a switch to anaerobic metabolism) will be less severe under the increased temperature, and that under a scenario of thermal adaptation the effects will be smaller when larvae are reared at their corresponding mean summer water temperature.

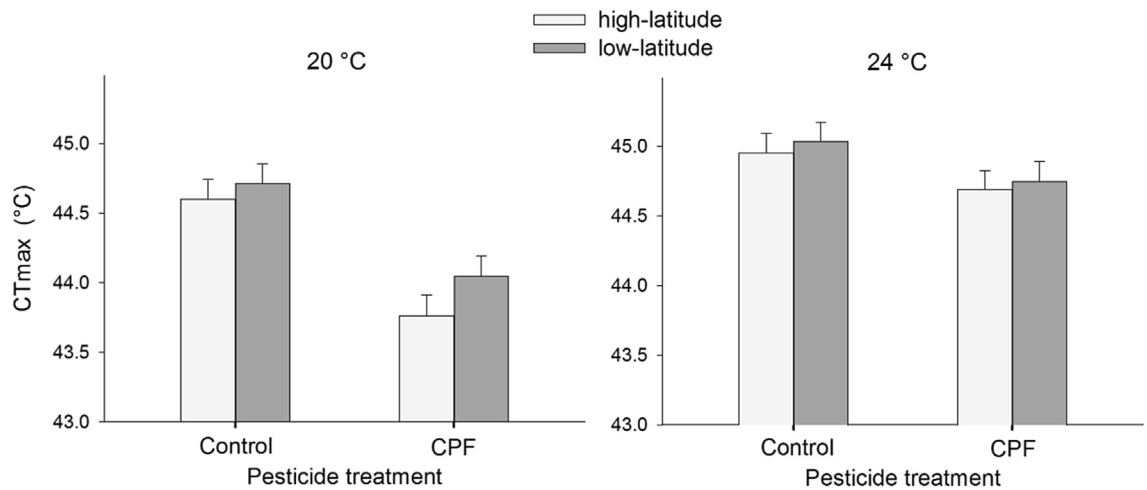

Fig. 1. Upper thermal tolerance (measured as critical thermal maximum, CTmax) of *Ischnura elegans* larvae as a function of chlorpyrifos exposure, rearing temperature and latitude of origin. Means are given with 1 SE.

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