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The Effect of Acclimation Temperature on the Critical Thermal Maximum of a Cold-water Population of *Pteronarcys dorsata* (Say) (Plecoptera: Pteronarcyidae)

Logan Shoup^{1,2} and David C. Houghton^{1,*}

Abstract

The critical thermal maximum (CT_{max}) of *Pteronarcys dorsata* (Say) acclimated in the laboratory to 5 different temperatures ranging from 4 to 28°C was 34.7–36.6°C. A 6th temperature (33°C) resulted in 100% mortality during the acclimation period. Although its CT_{max} values rank *P. dorsata* as moderately sensitive to thermal stress, the < 2°C difference over a 7-fold increase in acclimation temperature suggests only a weak ability to adapt to warming conditions relative to other tested aquatic insect species. This stenothermy in *P. dorsata* was likely due to the consistently cool stream in which this populations lives. Our results suggest that cold-water populations are particularly susceptible to thermal alterations. They also provide the first CT_{max} values for a species of pteronarcyid stonefly and the first of any aquatic insect over such a wide range of acclimation temperatures.

Temperature is widely recognized as one of the most important variables influencing the distribution and ecology of aquatic organisms, nearly all of which are exothermic (Caissie 2006, Haidekker and Hering 2008, Dallas and Rivers-Moore 2012). Many anthropogenic activities increase the temperature of freshwater ecosystems, for example: heated discharges from industrial sites or agriculture (Lessard and Hayes 2003), removal of riparian vegetation with subsequent increase in sunlight penetration (Rutherford et al. 1997, Houghton et al. 2013), removal of groundwater and other subsurface changes (LeBlanc et al. 1997), and the developing effects of anthropogenic climate change (Daufresne et al. 2004). These concerns necessitate studies that determine high temperature tolerances of freshwater organisms, especially in light of the current documented decline of such organisms (Ricciardi and Rasmussen 1999, De Walt et al. 2005, Houghton and Holzenthal 2010).

Unfortunately, knowledge about high temperature tolerances of aquatic organisms, especially those of aquatic insects, is still lacking. The most comprehensive study (Dallas and Rivers-Moore 2012) documented upper temperature tolerances for 23 South African insect families within the aquatic Coleoptera, Hemiptera, Diptera, Megaloptera, Plecoptera, Ephemeroptera, and Trichoptera. Most of their specimens, however, were not identified to the species level. For North American aquatic insects, laboratory studies on upper temperature tolerance have been conducted on approximately 7 stonefly species (Heiman and Knight 1972, Ernst et al. 1984, Poulton et al. 1989), 12 caddisfly species (Nebeker and Lemke 1968, Gauvin and Hern 1971, deKozlowski and Bunting 1981, Moulton et al. 1993), 3 mayfly species (deKozlowski and Bunting 1981) and 2 dragonfly species (Garten and Gentry 1976).

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For most of these studies, high temperature tolerance has been defined non-lethally, through the determination of the critical thermal maximum, or CT_{max} (Cowles and Bogert 1944). CT_{max} is the temperature at which a predetermined non-lethal behavioral endpoint is reached. For aquatic invertebrates, this endpoint usually involves a loss of equilibrium or grip on the substrate (Dallas and Rivers-Moore 2012). CT_{max} is generally considered a more ecologically valuable endpoint than death, since its corresponding lower temperatures are more realistically encountered in the natural world, and are likely to induce more subtle and chronic effects on a population (Heiman and Knight 1972).

The temperature of laboratory acclimation before trials may account for the majority of variation in experimental CT_{max} (Ernst et al. 1984, Moulton et al. 1993, Dallas and Rivers-Moore 2012, Galbraith et al. 2012). For example, the caddisflies *Hydropsyche morosa*, (Hagen) (Hydropsychidae), *H. simulans* Ross (Hydropsychidae), and *Chimarra obscura* (Walker) (Philopotamidae), and the stonefly *Agneta capitata* (Pictet) (Perlidae) all exhibited increases in CT_{max} commensurate with increase in acclimation temperature (Ernst et al. 1984, Moulton et al. 1993). All four of these species are common in both cold-water and warm-water streams, display a wide geographic range, and are presumed to be eurythermic (Stewart and Stark 1988, Houghton 2012). In contrast, increasing the acclimation temperature of the spring-emerging stonefly *Isoperla namata* Frison (Perlodidae) did not result in a significant increase in CT_{max} (Ernst et al. 1984), even though it was found in the same river as the aforementioned *A. capitata*. The authors speculated that this observed stenothermy in *I. namata* resulted from the univoltine spring emergence of the species, and that summer-emergent or semivoltine species would likely have greater high temperature tolerance due to their regular exposure to warmer water temperatures during the summer.

The purpose of our study was to determine the effects of acclimation temperature on the CT_{max} of a semivoltine insect living in a cold-water stream environment. Our study organism, *Pteronarcys dorsata* (Say) (Pteronarcyidae), is a common inhabitant of cold-water streams throughout the eastern U.S. (Stewart and Stark 1988). Temperature has previously been shown to affect the nymphal feeding rate, adult emergence success, egg production, adult longevity, and general life cycle of the species (Nebeker 1971, Lechleitner and Kondratieff 1983). No study of CT_{max} , however, has been conducted on *P. dorsata*, or on any other species of pteronarcyid stonefly.

Materials and Methods

The Little Manistee River (N44.02°, W85.63°) is a third-order stream site located in the northwestern portion of the Lower Peninsula of Michigan. Due to its relatively undisturbed watershed and stable groundwater input, the Little Manistee is one of the coldest and most stable streams in the Lower Peninsula (Tonello 2005). It hosts potamodromous spawning runs of steelhead [*Oncorhynchus mykiss* (Walbaum)], Chinook salmon [*Oncorhynchus tshawytscha* (Walbaum)], and brown trout (*Salmo trutta* Linnaeus) from Lake Michigan, and contains breeding populations of brook trout [*Salvelinus fontinalis* (Mitchill)] (Seelbach 1993).

Late instar (> 2cm body length) *P. dorsata* specimens were collected from the Little Manistee by hand from late June to late September 2012, transported to the lab in Styrofoam coolers filled with river water, and housed for 36 hours in a Frigid Units Living Stream™ (www.frigidunits.com) set to ambient photoperiod. Groups of specimens were acclimated to one of six temperatures: 4, 10, 16, 22, 28, and 33°C. Specimens were taken directly from stream temperature to acclimation temperature, except for two trial groups of 33°C specimens which were gradually warmed up over 30-60 minutes in an 850 ml bowl floated in the Living Stream. Summary data for trial groups are in Table 1.

To determine CT_{max} , each trial group was placed in a Julabo MB-13 circulating heated water bath (www.julabo.com) set to 40% external and 60% internal circulation. The device was linked to a computer using Julabo EasyTemp™ software, allowing for precise programming and logging of temperature protocols. In each trial, specimens were placed into the bath containing Living Stream water, given 1x1 mm latex window screen to use as substrate, and allowed to orient themselves relative to the current for 5 minutes before the temperature was raised. Water temperature began at the acclimation temperature and was raised by 0.34°C per minute (Dallas and Rivers-Moore 2012) until CT_{max} was reached for all trial specimens. CT_{max} was defined as the loss of ability to cling to the substrate. Specimens that were temporarily dislodged by the current or by other specimens were not removed from the water bath if they were able to re-attach and assume a normal posture. Removed specimens were placed into an 850 ml bowl which was floated in the Living Stream to cool specimens back to acclimation temperature over a 30–60 minute period. Once acclimation temperature was reached, specimens were returned to the Living Stream and their survival checked at 24 and 48 h. Voucher specimens were deposited in the Hillsdale College Insect Collection.

River temperature and dissolved oxygen saturation were measured during the afternoon of the hottest day of a particular week throughout our sampling period using a YSI-55 handheld digital probe (www.ysi.com) in the same consistently sunny midstream location. It was not our intention to determine the representative thermal profile of the Little Manistee River. Instead, we wanted to document the warmest temperatures that *P. dorsata* would be exposed to in its natal habitat.

Results

Nymphal mortality was 100% at 33°C during the acclimation period of all four trials. Nymphal acclimation mortality was 0% at the other temperatures (Table 1). Mean CT_{max} for the 4–28°C acclimation temperature groups ranged from 34.7 to 36.6°C (Fig. 1). CT_{max} did not correlate with either acclimation temperature ($r^2 = 0.18$, $P = 0.50$) or stream temperature during specimen collection ($r^2 = 0.25$, $P = 0.20$). There was also no correlation between ambient and acclimation temperature ($r^2 = 0.12$, $P = 0.90$). Somewhat conversely, both acclimation temperature ($F = 8.6$, $df = 1$, $P = 0.004$) and date ($F = 8.0$, $df = 1$, $P = 0.006$) explained significant variation in CT_{max} , whereas ambient temperature did not (Generalized Linear Fixed Model, $F = 8.1$, $df = 3$, $P < 0.001$). Mean post-trial survival of specimens over 48 hours was lower in the 28°C group (= 69%) than in the other groups (= 100%, 1-way Analysis of Variance with *Post-hoc* Tukey test on ArcSine transformed data, $F = 3.57$, $df = 5$, $P = 0.03$) (Table 1). Little Manistee River temperatures only exceeded 20°C on one measurement day; otherwise temperatures were ~13–20°C with > 90% dissolved oxygen saturation (Fig. 2).

Discussion

One of the fundamental criticisms of CT_{max} studies is that organisms are being tested experimentally at temperatures higher than will be encountered in the wild, thus the relevance of CT_{max} to survival in natural thermal regimes is not clear (Lutterschmidt and Hutchison 1997, Galbraith et al. 2012). Dallas and Rivers-Moore (2012) argue that the real value of CT_{max} studies is not in the ‘significance’ of a particular result, but rather in the comparisons of the responses of organisms to those of other organisms. They use this approach to identify several particularly stenothermic families that may be useful as thermal bioindicators.

The CT_{max} for *P. dorsata* was fairly high relative to that of other stoneflies. Relative to other aquatic insects in general, *P. dorsata* would be rated as ‘moderately sensitive’ (Dallas and Rivers-Moore 2012). We suspect, however, that

Table 1. Summary data from *P. dorsata* CT_{max} trials during 2012. 'Stream temperature' was the temperature of the Little Manistee River at the time of specimen capture.

Acclimation temperature	Trial #	n	Date	Stream temperature	Pre-trial survival	CT _{max}	24h survival	48 h survival
4°C	1	9	06 Aug	~18°C	100%	36.0°C	100%	100%
	2	7	06 Aug	~18°C	100%	35.9°C	100%	100%
	3	15	11 Sep	~13°C	100%	35.9°C	100%	100%
10°C	1	5	06 July	~22°C	100%	34.5°C	100%	100%
	2	8	06 July	~22°C	100%	35.4°C	100%	100%
	3	10	06 July	~22°C	100%	34.2°C	100%	100%
16°C	1	5	30 June	~18°C	100%	35.7°C	100%	100%
	2	9	30 June	~18°C	100%	34.2°C	100%	100%
	3	6	30 June	~18°C	100%	34.6°C	100%	100%
22°C	1	7	25 Jul	~19°C	100%	36.6°C	100%	100%
	2	8	25 Jul	~19°C	100%	36.4°C	100%	100%
	3	12	25 Jul	~19°C	100%	36.5°C	100%	100%
28°C	1	10	14 Aug	~15°C	100%	36.6°C	100%	100%
	2	10	14 Aug	~15°C	100%	36.6°C	60%	40%
	3	9	19 Sep	~13°C	100%	35.8°C	79%	67%
33°C	1	14	29 Aug	~13°C	0%	n/a	n/a	n/a
	2	13	29 Aug	~13°C	0%	n/a	n/a	n/a
	3	8	29 Sep	~13°C	0%	n/a	n/a	n/a
	4	11	29 Sep	~13°C	0%	n/a	n/a	n/a

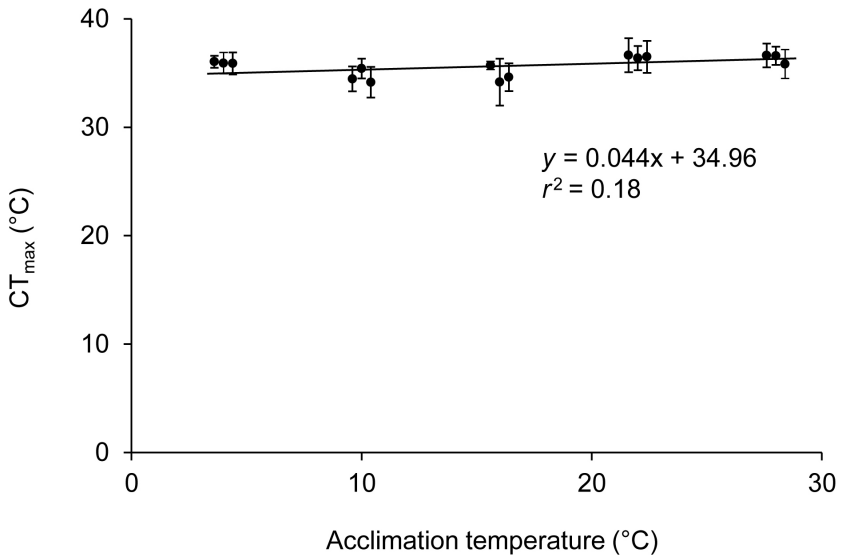


Figure 1. Mean (\pm SD) CT_{max} values for *Pteronarcys dorsata* acclimated to 5 different temperatures and their correlation with acclimation temperature. Markers are slightly offset for clarity.

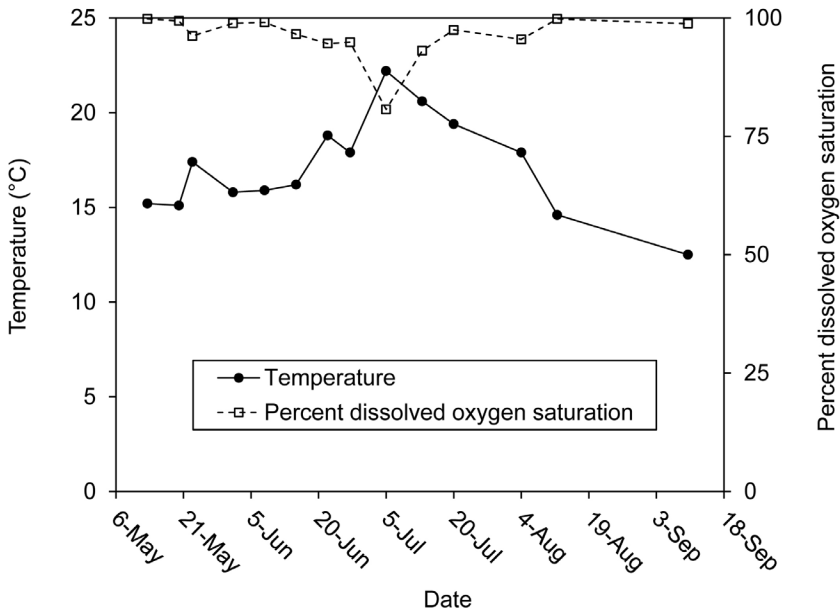


Figure 2. Temperature and dissolved oxygen levels for the Little Manistee River during May–September 2012. Data were collected from a sunny midstream site during afternoons of the hottest day of a particular week.

CT_{max} may be artificially high in *P. dorsata* due to its large (> 2 cm in length) size. *Pteronarcys* specimens are some of the largest stoneflies, and are larger than nearly any previously tested aquatic insect (Dallas and Rivers-Moore 2012). Larger organisms take longer to heat up, and so core temperature of the tested specimens may have lagged behind that of the water bath (Lutterschmidt and Hutchison 1997). Dragonflies, the other insects of similar size as *P. dorsata*, tend to have very high CT_{max} (Garten and Gentry 1976, Dallas and Rivers-Moore 2012).

Some of the statistical incongruity in our acclimation results may be due to overly sensitive statistical tests that do not reflect biological significance (Hillborn and Mangel 1997), and some may be due to our experimental design. Due to logistical constraints, we were able to acclimate groups of *P. dorsata* to only a single temperature at a time. Thus, there is potential concern over variable covariance. For example, if nymphs from relatively warm ambient temperatures were acclimated to warm temperature in the lab, the ultimate source of CT_{max} differences would be difficult to ascertain. The lack of correlation between our ambient and acclimation temperatures, however, as well as the lack of significance of ambient temperature as a predictor variable, suggested that this concern was of minimal importance.

Instead, our results suggested that date may have confounded acclimation results, possibly due to developmental differences between the tested specimens. Garten and Gentry (1976) found that, within the same environment, larger species of dragonflies had higher CT_{max} than smaller species, suggesting that older instars may have higher CT_{max} than younger ones. Conversely, Heiman and Knight (1972) found smaller nymphs of *Paragnetina media* Walker (Plecoptera: Perlidae) had higher CT_{max} than larger nymphs. They attributed this difference, however, more to the effects of gender than size specifically. Both studies found that the effects of acclimation temperature were more important than that of size.

While questions remain about statistical and biological significance, as well as those of potential covariance, the most striking result of our study is the overall lack of difference in CT_{max} between *P. dorsata* trials given the wide range of acclimation temperatures specimens were exposed to. In previous aquatic insect studies, acclimation temperature increases of 1.5–2.5× have resulted in a 3–5°C increase in CT_{max} (Ernst et al. 1984, Moulton et al. 1993, Dallas and Rivers-Moore 2012, and our own unpublished data). The exception, the aforementioned *Isoperla namata* Fison, increased in CT_{max} only 0.6°C after a 2.5-fold increase in acclimation temperature. The difference in mean CT_{max} between our acclimation temperature groups was < 2°C despite a 7-fold increase in acclimation temperature from 4°C to 28°C. No previous study has reported more than 2 acclimation temperatures, and only one—on corduliid dragonflies (Garten and Gentry 1976)—acclimated specimens to temperatures > 19°C. Thus, it is not possible to compare the full range of response of *P. dorsata* to other species. It does appear, however, that the Little Manistee River population of *P. dorsata* is stenothermic relative to most other tested aquatic insects.

This lack of ability to acclimate and raise its CT_{max} in *P. dorsata* is likely related to its consistently cold-water habitat of the Little Manistee River (Tonello 2005). The junior author has been studying the river for three years (e.g., Houghton et al. 2013) and has never previously observed temperatures at the study site above 20°C. Indeed, the only day we recorded a temperature > 20°C during our study occurred on a July afternoon in a sunny midstream location after three days of record-breaking (> 35°C) warm air temperature (www.weatherunderground.com).

Our high rate of survival of *P. dorsata* specimens at the lower acclimation temperatures 48 hours after trials validates our CT_{max} endpoint (Lutterschmidt and Hutchison 1997). The lower survival in the 28°C acclimation group suggests that those specimens were approaching their thermal tolerance limit. It is not

clear if their mortality was caused by the stress of the CT_{max} trial, accumulated stress caused by the time spent at 28°C, or both. The abrupt change of temperature from ~15°C in the field to 28°C in the Living Stream during acclimation may have had a chronic effect on specimens, even though there was no acute mortality. Due to this concern, we warmed up the last two 33°C trial groups gradually to acclimation temperature. Both gradual and abrupt temperature change to 33°C, however, resulted in 100% mortality within the acclimation period, suggesting that temperature was simply higher than the thermal tolerance limits of *P. dorsata*. Nebecker and Lemke (1968) found exposure to 29.5°C for 96 hours resulted in 50% mortality for *P. dorsata*.

Pteronarcys dosata is generally considered to exhibit a semivoltine life cycle, although a southwestern Virginia population has been documented as univoltine, presumably due to its exposure to water temperatures > 20°C from May to September (Lechleitner and Kondratieff 1983). Although we do not have comprehensive life cycle data for the Little Manistee River population, we suspect a two-year cycle due to the presence of two distinct nymphal size classes found throughout the summer. Ernst et al.'s (1984) assertion that semivoltine insects are likely to be eurythermic due to exposure to warm summer temperature probably does not apply to our *P. dorsata* population due to the consistently cool stream temperatures of the Little Manistee. Likewise, our results suggest that cold-water populations of aquatic insects are particularly stenothermic and susceptible to thermal alterations even if the species has the physiological capacity for higher thermal tolerance in other habitats.

Substantial further research remains to be conducted on these topics. It would be interesting to compare the CT_{max} from the Little Manistee population of *P. dorsata* to that of the aforementioned southwestern Virginia population that is routinely exposed to > 20°C temperatures. Likewise, exploring chronic effects (e.g., mortality, sublethal effects, or adaptation) of thermal stress on *P. dorsata* and other cold-water populations may be a more realistic prediction of thermal alteration. More basically, thermal tolerance studies of any type have been conducted on < 1% of North American aquatic insects and considerable work needs to be done.

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