

Temperature response of growth of larval dragonflies – an overview

Frank Suhling*, Ida Suhling and Otto Richter

Institut für Geoökologie, Technische Universität Braunschweig, Langer Kamp 19c, 38106 Braunschweig, Germany

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This article is dedicated to Georg Ruppell for his 75th birthday. Thanks for the friendship and inspiration!

We review the knowledge about the thermal reaction norms of larval growth in Odonata with a focus on the temperature response function. We re-analyze literature data and present our own results on growth rates of larvae of 14 species of Libellulidae reared at different temperatures. Temperature response curves (TRC) were fitted in order to estimate two relevant components of the thermal reaction, namely the optimum temperature for growth (T_{opt}) and the increase of growth rate with temperature (Q_{10}). We also examined what is known about the thermal minimum (T_{min}) and the thermal maximum (T_{max}) for growth to delimit the thermal ranges of odonates. All information indicates that larval growth is generally warm adapted, with species-specific variation of T_{opt} of 21–31°C, T_{min} of 8–12°C, and T_{max} of up to 44°C (the latter being the upper lethal limit, the true T_{max} for growth remains unknown). The values of Q_{10} distinguish some more specialized species, mostly with high T_{opt} and of tropical origin, and others being more thermal generalists, often being temperate species and/or from lotic habitats. We examine some biotic and abiotic factors affecting the temperature response of growth and we discuss the temperature response in the light of global warming.

Keywords: temperature response; larval growth; climate warming

Introduction

Temperature is perhaps the most important variable affecting the ecophysiological performance of ectotherms (Angilletta, Niewiarowski, & Navas, 2002). Most species are adapted to particular temperature ranges, and temperature is often a major environmental factor influencing their distribution (Trudgill, Honek, Li, & Van Straalen, 2005). Accordingly, temperature is regarded as a proximate predictor for modeling species distribution and its response to climate change (Elith & Leathwick, 2009), but often without fully understanding the mechanisms. In order to reveal how organisms respond to the thermal environment we need to understand thermal response of biological processes (Dell, Pawar, & Savage, 2011). This requires information about the response of ecophysiological processes, such as growth, to changing temperature. The general principle is long known: within the thermal range of a species, as the temperature decreases the rates of development slow down to a lower thermal limit where development ceases. As temperature

*Corresponding author. Email: f.suhling@tu-bs.de

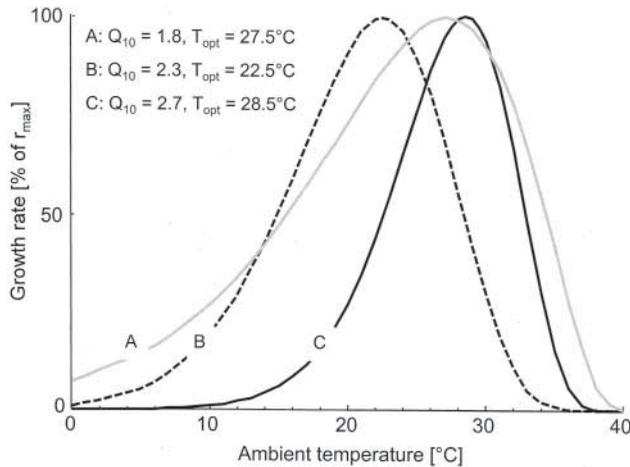


Figure 1. Temperature response curves of growth in larval Odonata. The three examples represent three types (A and C our data, B re-analyzed from Krishnaraj & Pritchard, 1995): (A) *Orthetrum coerulescens*, with low Q_{10} , hence relatively high growth rate over a wide range of temperatures; (B) *Coenagrion resolutum*, with high Q_{10} (thermally more specialized) and relatively low thermal optimum (T_{opt}); and (C) *Crocothemis erythraea*, with high Q_{10} and high T_{opt} , thus a high-temperature specialist. The growth rates are transformed to % of maximum growth rate to make the curve-shapes more easily comparable. The measured growth rates are omitted for convenience. Note that the O'Neill function used to fit the curves does not consider a possible lower thermal limit for growth; this will be discussed later.

increases, the rates of development increase up to a temperature optimum, above which they again decrease and eventually cease at an upper temperature limit (reviews in Dell et al., 2011; Dixon et al., 2009; Trudgill et al., 2005). Such temperature response curves (TRC), also termed thermal performance curves, are used to describe how the expression of traits, e.g. growth rate, varies as a function of temperature. A TRC can be constructed by measuring trait values across a range of temperatures for a single species. Relevant components that describe the temperature response are the upper and the lower thermal limits (T_{max} and T_{min}), the optimal temperature where the growth rate is highest (T_{opt}), and the increase of growth rate with increasing temperature below T_{opt} , usually measured over intervals of $10^{\circ}C$ (Q_{10}). The function has a typical – usually asymmetric – shape. There are good arguments that the optimal growth rate may in some circumstances be lower than the maximum possible growth rate, and that high growth rates are costly, for instance due to increased mortality at maximum growth rates (Dmitriew, 2011). However, optimal growth rate would depend very much on the various environmental conditions a species may encounter and is thus very difficult to compare between species in a standardized approach.

The components of the TRC have specific values which can be used to describe the type of thermal adaptation of species or populations. Considerable genetic variation in thermal reaction norms exists within and among species (Angilletta et al., 2002). A species can be considered a thermal generalist if it has a low value of Q_{10} , and a specialist if Q_{10} is high. A specialist may be cold (low T_{opt}) or warm (high T_{opt}) adapted. Figure 1 shows examples of different types of TRC for larval growth in Odonata.

Taking the relevance of temperature into account it may be surprising that TRCs of most ecophysiological traits of Odonata are not very well investigated. Even Corbet's (1999) book provides only scattered information on temperature responses of Odonata. However, the response of many traits to the ambient temperature is investigated in at least some species. For instance, vertical flight force (Marden, 1995) and wing stroke frequency (May, 1981), and egg laying rates increase with temperature (Martens, 1993; McVey, 1984). Odonate eggs have generally high optimum temperatures and do not develop below $10^{\circ}C$ (Pritchard, Harder, & Mutch, 1996; Rotvit

& Jacobsen, 2013). Because the egg development shows little adaptation to latitude Odonata are supposed to be of tropical origin (Pritchard et al., 1996). Thus, one may also presume warm adaptation in larval growth (e.g. Leggott & Pritchard, 1985).

In this article we focus on the response of larval growth rate to temperature. We express growth as the increase of size. The growth rate is the size increase over a distinct period of time of continuous growth; periods when growth is stopped due to an induced diapause are not counted for estimating growth rate. This differs from development rate, which is usually expressed as 1/development time and thus includes periods where growth has stopped. Besides growth the development rate also involves other variables such as all ontogenetic changes in morphology (Corbet, 1999, p. 214). Particularly in many temperate dragonflies, seasonal changes in photoperiod cause variation in speed of development, including possible interruptions, for instance over the winter months (Corbet, 1999, p. 226). The relevance of photoperiod response for voltinism (duration of development) has been emphasized (Corbet, Suhling, & Soendgerath, 2006). The induction of diapause via photoperiodic signals seems to happen in certain instars (winter critical size). This is probably genetically determined, but when it is reached is widely influenced by the growth rate influenced by exogenous factors, mainly temperature and food (Corbet, 1999, p. 212).

Thus, investigating the species-specific relations between growth and temperature is important, particularly for understanding and predicting how odonate development will respond to warming environments. In only very few species have TRCs of growth been investigated under controlled conditions (e.g. Krishnaraj & Pritchard, 1995; Pritchard, Harder, Kortello, & Krishnaraj, 2000). This is typically done by observing the trait when the organism is kept under several fixed temperature conditions. The aim of this article is to collate what is known about the temperature dependence of growth in Odonata and specifically about the components T_{\max} , T_{\min} , T_{opt} and Q_{10} of the TRC. We particularly intend to examine the variation of these components between species, but also compare populations where possible. Besides literature data we also make use of unpublished data of our own experiments to estimate T_{opt} and Q_{10} for several Libellulidae. Finally, we discuss possible consequences at the community level caused by global warming under the assumption that TRC differs between species.

Temperature response model

There are various models used in order to fit temperature-dependent growth rate data (i.e. produce TRC), from simple Gaussian and polynomial models to more complex functions (cf. Damos & Savopoulou-Soultani, 2012; Dixon et al., 2009; Krenk et al., 2011). We decided to use only one model for all species to make the results comparable. We selected the O'Neill function (Spain, 1982):

$$\Phi(T) = k \left(\frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} \right)^p \exp \left(\frac{p(T - T_{\text{opt}})}{T_{\max} - T_{\text{opt}}} \right), \quad (1)$$

with $p = \frac{1}{400} J^2 \left(1 + \sqrt{1 + \frac{40}{J}} \right)^2$ and $J = (Q_{10} - 1)(T_{\max} - T_{\text{opt}})$.

This function provides a meaningful model since it incorporates three of the four components of the temperature response as defined above (T_{opt} , T_{\max} , Q_{10}) and therefore enables their direct estimation (examples for curve fits are depicted in Figure 2). In detail, the function takes into account that the rate of growth should rise with increasing temperature to an optimal temperature (T_{opt}) where growth rate is highest (k is the maximum growth rate), and drop again after this peak. Besides this, the equation includes the factor by which the growth rate is changed as a consequence of the rise in temperature before reaching the peak growth rate

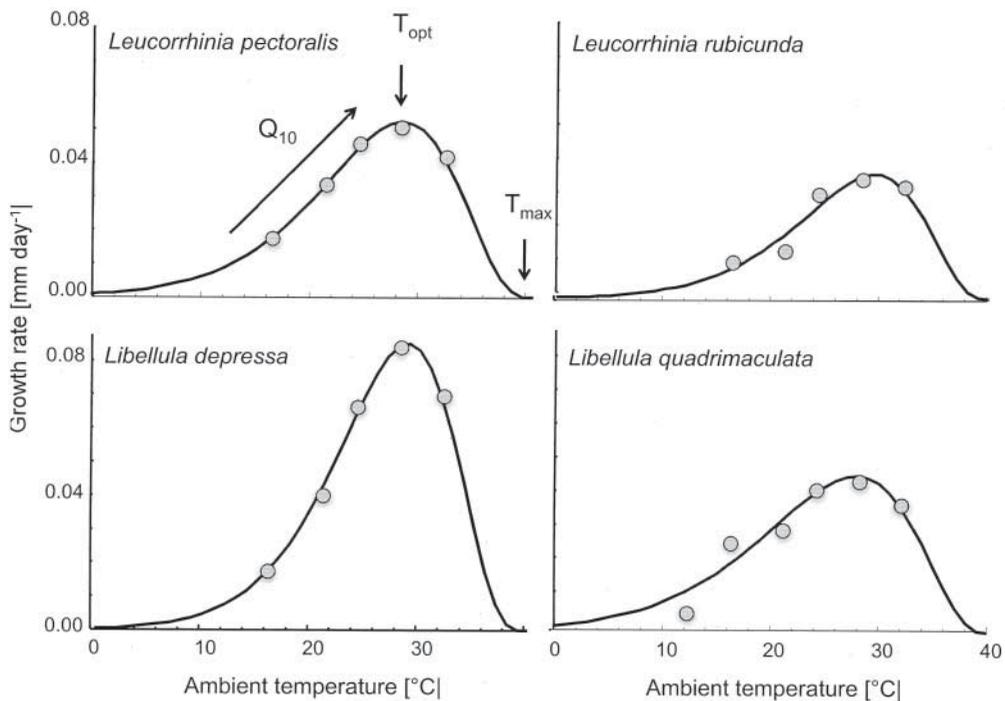


Figure 2. Examples for data fit using the O'Neill function. The gray dots are the data points for growth rates measured at the different temperatures; the line denotes the temperature response curve. The components T_{opt} , T_{max} , and Q_{10} are indicated.

(Q_{10}). T_{max} is the maximum temperature where growth is possible, T is the ambient temperature and $\phi(T)$ the respective mean growth rate from experimental data. We used this model to estimate Q_{10} and T_{opt} from known data on growth rates measured at different values of T . This was done by an algorithm implemented in many program systems, e.g. the nonlinear model fit (nlm in Mathematica) or nonlinear least square (in R). We used a script written in Mathematica (www.wolfram.com) and thus the nlm.

In most experiments, growth rates at temperatures above the optimum temperature are difficult to assess because of enhanced mortality. Therefore, most data sets include only one or two points above optimum temperature, if any at all. This poses some difficulties for parameter estimation concerning T_{max} . There are two possibilities to achieve convergence. One option is to define a constrained parameter estimation problem by introducing an upper bound for T_{max} , for instance 47°C, the upper thermal limit for insects (Addo-Bediako, Chown, Steven, & Gaston, 2000) for which also the nlm could be used. However, we did not make the attempt to estimate the T_{max} since experimental temperatures were usually not high enough to match the upper thermal limit for growth. Instead we used 40°C as a default setting for all fits, which is well within the range expected for Odonata (see discussion below). Test runs with the nlm indeed showed that 40°C is a very likely value. One important component describing the thermal range for growth, the lower thermal limit (T_{min}) is not considered in the model, which will be discussed below.

Data sources

Information on T_{max} and T_{min} was collated from various sources in the literature (see below). For estimating T_{opt} and Q_{10} we applied the O'Neill function described above and used two different

sources of data. One source was data from various publications which we re-analyzed (Table 1). In most cases the original data were not available to us. Thus, we scanned the figures showing growth rates at different temperatures and measured the distances of the data points from the axis by using the image analyzer software ImageJ (National Institutes of Health, USA, Version 1.44). This method is certainly not precise and the values may not be identical to the original ones. However, we suppose that for getting estimates of the requested TRC components it is sufficient. The rearing conditions, as far as we could reconstruct them from the literature, are listed in Supplement 1. The second source was our own data on growth rates of young instar larvae of 14 libellulid species. Some were collected from different populations and analyzed separately. All were reared at five different ambient temperatures at least: 16, 20, 24, 28, and 32°C, some also at 12°C. For a detailed description of the methods see Supplement 2.

We had two criteria for data sets to be used: (1) there had to be growth rates measured at least at four different temperatures; fewer different temperatures rarely revealed good fits. The span of rearing temperatures from the lowest to the highest values ranged from 8°C to 25°C. (2) The highest temperature treatment had to be above the peak of the growth rate, i.e. the value for growth rate at the highest temperature used had to be no higher than the previous value. This was usually the case in our own studies at 32°C. A few data sets used did not match this criterion, which weakens the estimates of T_{opt} , which is then noted in Table 1. Not all studies used the same measure for growth rate (see Supplement 1); but most studies measured change of size (mostly head width) over time.

An overview on the components of the TRC

The thermal optimum for growth (T_{opt}) and the Q_{10}

We only found 10 data sets in the literature that matched our relatively weak pre-conditions for fitting TRC, seven for Zygoptera and three for Anisoptera. We therefore also used two additional data sets for Zygoptera with four temperatures but no values above peak growth, and two data sets with only three temperatures, but one above peak growth (Van Doorslaer & Stoks, 2005a, 2005b). Together with our own data we fitted TRC for 25 species allowing us to estimate T_{opt} and Q_{10} (Table 1). The optimum temperature of all dragonfly species considered here is well above 20°C (Table 1). Some species of *Coenagrion* had the lowest values of T_{opt} , which were still above 21°C. However, even in the same genus, species with T_{opt} above 26°C occur, although these results have to be taken with some caution (cf. Table 1). In the family Coenagrionidae the variation is high; the highest value was that of *A. abbreviatum* at 31.9°C. All Libellulidae had T_{opt} above 26°C, most even above 28°C, with highest values around 30°C. Thus, they have relative high temperature demands for maximum growth, independently of their geographical origin. This is even true for *L. dubia*, a species with a mainly boreal distribution which had T_{opt} of 28°C even in a population living close to the Arctic Circle at 64° north. However, one has to take into account that *L. dubia* lives among *Sphagnum* mosses in peat bogs, hence experience very high temperature in their microhabitats (Sternberg, 1994) which is important to be able to grow enough during the short polar summer.

Odonate larvae are well known to increase growth rate with rising temperature, given sufficient food provided (Pickup & Thompson, 1990; Pickup, Thompson, & Lawton, 1984). This increase (i.e. the Q_{10}) defines whether a species is a thermal generalist or a thermal specialist concerning growth. For Coenagrionidae the Q_{10} values ranged between 1.7 and 2.3; one species, *C. hastulatum*, has Q_{10} as low as 1.5 (but only three data points, which weakens the result). Since only information on the increase of growth rate with rising temperature is required for Q_{10} we consider results on *I. elegans* from three populations (Shama, Campero-Paz, Wegner, De

Table 1. An overview of values of T_{opt} and Q_{10} (both \pm SE) for Zygoptera based on data of larval growth rates from at least four different temperatures. All data sets were analyzed or re-analyzed by using the O'Neill function; the R^2 is the goodness of fit. For details on rearing conditions see Supplements 1 and 2.

Family	Species	Origin	Latitude	T_{opt} [°C]	SE	Q_{10}	SE	R^2	Source	
Lestidae	<i>Lestes disjunctus</i> (Selys) *	Canada	51.1	24.8	0.3	2.3	< 0.1	0.99	1	
Coenagrionidae	<i>Amphiagrion abbreviatum</i> (Selys)	Canada	51.1	31.9	2.7	1.7	0.2	0.94	2	
	<i>Argia vivida</i> Hagen	Canada	51.5	27.6	0.3	2.0	0.1	0.99	2	
	<i>Coenagrion hastulatum</i> (Charpentier)	Sweden	63.5	21.8	–	1.5	–	–	3	
	<i>Coenagrion mercuriale</i> (Charpentier)	France	42.0	24.1	0.8	2.0	0.1	0.99	4	
	<i>Coenagrion puella</i> (Linnaeus)	Belgium	50.9	21.2	–	1.7	–	–	3	
	<i>Coenagrion puella</i> (Linnaeus)	Austria	48.3	22.9	0.9	2.2	0.2	0.86	5	
	<i>Coenagrion pulchellum</i> (Vander Linden) *	Belgium	51.0	27.5	1.0	2.0	0.1	0.99	4	
	<i>Coenagrion resolutum</i> (Selys)	Canada	51.5	22.5	0.4	2.3	0.1	0.99	1	
	<i>Coenagrion scitulum</i> (Rambur)	France	42.0	26.3	3.2	1.8	0.2	0.99	4	
	<i>Enallagma vesperum</i> Calvert	USA	43.4	24.3	0.3	2.1	0.1	0.97		
	<i>E. vesperum</i> [with predator]	USA	43.4	26.9	2.6	1.9	0.5	0.67	6	
	Aeshnidae	<i>Anax junius</i> (Drury)	Canada	43.5	29.3	0.5	1.9	0.1	0.99	7
	Libellulidae	<i>Crocothemis erythraea</i> (Brullé)	Germany	52.3	28.5	0.5	2.7	0.3	0.95	9
		<i>Crocothemis sanguinolenta</i> (Burmeister)	Namibia	– 21.8	26.3	0.7	2.0	0.2	0.90	9
<i>Diplacodes lefebvrii</i> (Rambur)		Namibia	– 21.8	30.7	0.6	2.1	0.1	0.99	9	
<i>Leucorrhinia dubia</i> (Vander Linden)		Sweden	63.9	28.2	0.4	2.1	0.1	0.96	9	
<i>L. dubia</i>		Sweden	59.9	27.0	0.1	1.9	< 0.1	0.99	9	
<i>L. dubia</i>		Sweden	57.0	28.1	0.3	2.2	0.1	0.99	9	
<i>L. dubia</i>		Germany	54.0	26.3	0.6	2.1	0.1	0.96	8	
<i>L. dubia</i>		Germany	52.6	28.6	0.8	2.4	0.3	0.92	9	
<i>Leucorrhinia pectoralis</i> (Charpentier)		Germany	52.3	28.1	0.3	2.0	0.1	0.99	9	
<i>Leucorrhinia rubicunda</i> (Linnaeus)		Germany	52.6	29.4	1.1	2.1	0.3	0.91	9	
<i>L. rubicunda</i>		Germany	54.0	26.4	0.3	2.2	0.1	0.99	8	
<i>Libellula depressa</i> Linnaeus		Germany	52.3	28.8	0.27	2.2	0.1	0.99	9	
<i>Libellula quadrimaculata</i> Linnaeus		Germany	52.6	27.9	1.07	1.9	0.2	0.90	9	
<i>Orthetrum cancellatum</i> (Linnaeus)		Germany	52.3	30.0	0.21	2.1	< 0.1	0.99	9	
<i>O. cancellatum</i>		France	43.5	27.1	0.79	2.1	0.2	0.92	9	
<i>Orthetrum coerulescens</i> (Fabricius)		Sweden	57.0	27.1	0.77	1.8	0.2	0.89	9	
<i>O. coerulescens</i>		Germany	52.3	26.8	0.36	2.2	0.1	0.94	9	
<i>Orthetrum trinacria</i> (Selys)		Namibia	– 21.8	29.9	0.83	2.2	0.2	0.97	9	
<i>Sympetrum striolatum</i> (Charpentier)		Germany	52.3	28.4	0.93	1.9	0.2	0.94	9	
<i>Sympetrum vulgatum</i> (Linnaeus)		Germany	52.3	26.6	0.61	1.9	0.1	0.92	9	
<i>Tramea basilaris</i> (Palisot de Beauvois)	Namibia	– 21.8	29.7	0.31	2.4	0.1	0.99	9		

*Data sets without temperatures high enough to reduce growth rates; i.e. T_{opt} may be higher than estimated here. Sources: (1) Krishnaraj and Pritchard (1995); (2) Pritchard et al. (2000); (3) Van Doorslaer and Stoks (2005a, 2005b); (4) Nilsson-Örtman, Stoks, De Block, and Johansson (2012a, 2012b); (5) Waringer and Humpesch (1984); (6) Culler et al. (2014); (7) Trotter (1971); (8) Soeffing (1990); (9) own data.

Block, & Stoks, 2011), all having Q_{10} of 2.5 (estimated with O'Neill). Among the Libellulidae the range was from 1.8 to 2.7. The highest values of Q_{10} indicate the highest degree of thermal specialization and the lowest relatively high growth rates over a wide thermal range, hence more generalist species. The highest Q_{10} values are found in *C. erythraea* and *T. basilaris*, both having high T_{opt} , thus being high-temperature specialists. This may be adaptation to tropical origin as

well as to their (often temporary) pool habitats. The results for *A. junius* do not fit well here. Like *C. erythraea* it was taken from a very northern population but unlike *C. erythraea* it had low Q_{10} (but high T_{opt}). The reason may be that *A. junius* has a long history of entering higher latitudes for breeding and may thus be adapted to produce offspring under lower temperature conditions (cf. May, 2012; Trottier, 1971). Moreover, in its populations individuals of *A. junius* of multiple geographic origins are mixing, which may limit specialization (May & Matthews, 2008). In contrast, *C. erythraea* has recently (within the last 10 years) extended its range into the region where eggs were taken (cf. Ott, 2010). On the other side of the spectrum there are species with relatively high Q_{10} but lower T_{opt} , hence being more specialized to lower temperatures; the best example is *C. resolutum* from Canada. Libellulid species that occur in temperate and boreal zones all have comparably low Q_{10} , with the exception of the southernmost population of *L. dubia* (see discussion of intraspecific variation below). Thus, despite having high thermal demands for maximum growth, they are thermally relatively little specialized, and can grow well under suboptimal low thermal conditions. The same is true for the running water species independently of their origin (temperate: *O. coerulescens*; tropical: *C. sanguinolenta*).

Maximum growth rates (r_{max}) at T_{opt}

Many studies used larval growth rates as a standard trait for comparing performance of species between various environmental conditions and for interspecific comparisons (e.g. Johansson & Suhling, 2004; McPeck, 2004; Sniégula, Johansson, & Nilsson-Örtman, 2012; Stoks, De Block, & McPeck, 2005), some rearing larvae at different temperatures (Nilsson-Örtman et al., 2012b; Shama et al., 2011; Van Doorslaer & Stoks, 2005b). Although such comparisons may allow valuable insight into specific mechanisms, comparisons without knowing the whole TRC bear the risk of misinterpretations of the potential performance of a species. For instance, of two species reared at 25°C one may already be above its peak growth rate, another one still much below it (Table 1). Here, we briefly compare maximum growth rates at T_{opt} that are directly comparable, i.e. those measured in the same units (mm day^{-1}). In the Coenagrionidae the r_{max} varied from values of 0.1–0.2 mm day^{-1} (*Coenagrion* spp.) to 0.7 mm day^{-1} (*I. elegans*). In the Libellulidae the r_{max} varies from 0.03–0.05 mm day^{-1} (*Leucorrhinia* spp. and some *Orthetrum* spp.) to 0.17 mm day^{-1} (*T. basilaris*). Thus, there are very distinct differences in maximum growth rate, with species possessing the ability to reproduce in temporary waters, such as *C. erythraea*, *D. lefebvii*, and *T. basilaris*, reaching high growth rates at T_{opt} . Lower growth rates occur in perennial pond and lake species as well as in running water species, such as *O. coerulescens*. Thus, the perception of slow–fast life style dichotomy in Odonata (Johansson, 2000) is probably reflected here, with the major difference appearing to be between species living in permanent (slow) versus temporary habitats (fast) (cf. Johansson & Suhling, 2004).

The lower and upper thermal limits for growth (T_{min} , T_{max})

Dragonfly larvae are known to survive relatively low temperature. The lethal minimum is probably below 0°C in many species (Corbet, 1999, p. 187). Lethal levels for *C. resolutum* (Selys) and *C. angulatum* are at –5 to –6°C (Sawchyn & Gillot, 1975). However, it seems that for growth there is a minimum threshold well above such values. In *Argia vivida* from a hot spring Leggott and Pritchard (1985) did not observe any growth at 5°C and at 10°C larvae did not manage to attain instar 5. Even at 15° no larva was able to make it to the final instar. Thus, the T_{min} found for completing life cycle in *A. vivida* was estimated to be between 10 and 15°C and since the minimum temperature for egg development was found to be 11.25°C this was also set as T_{min} for larval development. Waringer and Humpesch (1984) found no growth of larval *C. puella* at 4, 8

and 10°C; only at 12°C and above growth was observed. *Leucorrhinia dubia* and *L. rubicunda* showed very low growth (between zero and one molt within 50 days) at 10°C, but more than two molts within 50 days at 15°C (Soeffing, 1990). Other studies imply that the lower thresholds for larval development is between 8 and 10°C, such as for *I. elegans* (Thompson, 1975), *A. junius* (Trottier, 1971), and *Leucorrhinia intacta* (Hagen) (Deacon, 1975 in Corbet, 1999). With our own experiments we cannot contribute much to this topic since the lowest temperature used was in most cases 16°C. But, *L. dubia* and *L. quadrimaculata* reared at 12°C exhibited little growth and not all individuals were growing at all. With only very few species investigated, all originating from temperate or even boreal populations, generalization seems ambitious. However, *A. vivida* is a more tropically based genus (Pritchard, 2008) and the study population was from a hot spring. Therefore, the results for *A. vivida* may represent tropical species. Thus, tentatively all data seem to point towards a T_{\min} for growth of around 10°C in odonate larvae, but for individual species or populations the threshold may be from 8 to 12°C.

There are no data available for the maximum temperature above which growth stops in Odonata. However, the upper lethal temperature (ULT) may serve as a substitute. The average ULT for insects was evaluated as $44.4 \pm 0.3^\circ\text{C}$ (Addo-Bediako et al., 2000). It can be expected that the T_{\max} for growth is lower than the ULT. The critical thermal maximum, i.e. the temperature above which most individuals respond with unorganized locomotion subjecting the animal to likely death, is usually also some degrees (2–5°C) lower than the ULT (Garten & Gentry, 1976; Leggott & Pritchard, 1986). In Table 2 all data known to us for ULT of Odonata are compiled. The values are higher than that of most other freshwater macroinvertebrates tested, except for coleopterans (Stewart, Close, Cook, & Davies, 2013) and upper thermal limits of above 40°C are obviously possible. It also appears that in many stream dragonflies the ULT is lower than in lentic water species (Garten & Gentry, 1976). But, it has to be taken into account that in the studies of Neberker and Lemke (1968) and Stewart et al. (2013) the larvae have been acclimated at low temperatures only (Table 2). Studies by Martin, Garten, and Gentry (1976) and Garten and

Table 2. Overview of upper lethal temperature (ULT) for Odonata larvae from various studies (as LT_{50} at 96 h). Mean values are presented where more than one acclimation temperature was used.

Family	Species	ULT (°C)	Habitat	Source	Acclimation temperature (°C)
Coenagrionidae	<i>Argia vivida</i> Hagen	44.4–46.0	Hot spring	Leggott and Pritchard (1986)	10–30
Aeshnidae	<i>Austroaeschna anacantha</i> Tillyard	33.9	Stream	Stewart et al. (2013)	15
Aeshnidae	<i>Boyeria vinosa</i> (Say)	33.0	Stream	Neberker and Lemke (1968)	10
Gomphidae	<i>Ophiogomphus</i> <i>rupinsulensis</i> (Walsh)	32.5	Stream	Neberker and Lemke (1968)	10
Corduliidae	<i>Epithecya cynosura</i> (Say)	42.7	Pond	Garten and Gentry (1976)	12–32
Corduliidae	<i>Neurocordulia alabamensis</i> Hodges	42.6	Stream	Garten and Gentry (1976)	12–32
Macromiidae	<i>Macromia illinoiensis</i> Walsh	43.1	Stream	Garten and Gentry (1976)	12–32
Libellulidae	<i>Celithemis</i> sp	42.4	Pond	Garten and Gentry (1976)	12–32
Libellulidae	<i>Ladona deplanata</i> Rambur	41.3	Pond	Garten and Gentry (1976)	12–32
Libellulidae	<i>Libellula auripennis</i> Burmeister	45.7	Thermal pond	Garten and Gentry (1976)	12–32
Libellulidae	<i>Pachydiplax longipennis</i> (Burmeister)	44.5	Thermal pond	Garten and Gentry (1976)	12–32
Libellulidae	<i>Plathemis lydia</i> (Drury)	43.2	Pond	Fritz and Punzo (1976) in Punzo (1988)	—*

*For Fritz & Punzo (1976) no information on acclimation was available.

Gentry (1976) indicate that the thermal maximum is positively correlated with the acclimation temperatures in which the larvae were raised (but Leggot & Pritchard, 1986 did not find such a correlation). At acclimation temperature of 12°C the stream species studied by Garten and Gentry (1976) also had distinctly lower thermal limits than those acclimated at 32°C. Thus, the stream aeshnids and gomphids listed in Table 2 may also survive higher temperatures than 33°C if living in warmer environments. Stewart et al. (2013) emphasize that aeshnids and gomphids have lower thermal limits than libellulids and corduliids. However, since no genera of these families are investigated which live in warmer environments, such as *Anax* or *Paragomphus*, this should be accepted with caution. The ULT for only one zygopteran is known to us and the population investigated was from a hot spring (Leggott & Pritchard, 1986), thus is probably not very representative. Species of Calopterygidae, which often have high oxygen demands (Zahner, 1959), probably have much lower ULT. On the other hand, more than 30% of *Copera annulata* (Selys) survived treatment at 35°C over 16 days (Chang, Zhai, Liu, & Wang, 2007).

Soeffing (1990) provided information about mortality of young instar larvae of *L. dubia* and *L. rubicunda* over 50 days. Although this is not fully comparable with the ULT shown in Table 2 it is of special interest for us because we reared the same two species. Soeffing (1990) found 100% mortality in *L. dubia* after 50 and in *L. rubicunda* after nine days of continuously 35°C and lowest mortality was between 20 and 25°C (*L. dubia* about 10%, *L. rubicunda* about 20%). We had about 75% mortality at 32°C over 30 days. In our attempts to fit the TRC we used 40°C as T_{\max} for all species, hence a higher value than the 100% mortality value reported by Soeffing (1990), but lower than the values for all other libellulids (Table 2). However, re-analyzing the data for *L. dubia* and *L. rubicunda* with a default T_{\max} of 35°C caused severely reduced goodness of fit, even with the data set of Soeffing (1990). Thus, we decided to keep the 40°C default setting.

Intraspecific variation

How much do the components of the temperature response we have discussed so far vary between populations? Table 1 shows some variation in T_{opt} or Q_{10} , and sometimes in both, where data from different populations are available. Shama et al. (2011) reported variation in growth rate increase with increasing temperature for *I. elegans* from three populations along a latitudinal gradient from southern France (43.5°N) to southern Sweden (55.65°N). But re-analyzing the data with the O'Neill function revealed only diminutive variation in Q_{10} , while growth rate varied distinctively between the French population, which is likely multivoltine, and the other two populations, which are probably not. Data on *L. dubia* from five sites along a latitudinal gradient of 11.6 degrees (Table 1) showed variation in T_{opt} by about 2°C and maximum growth rate differed even more drastically between the sites. The Q_{10} varied mostly between 1.9 and 2.2; only the value for the southernmost population was higher. In contrast, Nilsson-Örtman et al. (2012a) found trends to higher specialization in northern populations when comparing among and within populations of six species of *Coenagrion*. These divergent results indicate mainly that our understanding of these processes is premature. The reason for variation may be genetic as well as well as trait plasticity (review in Stoks, Geerts, & De Meester, 2013).

Factors affecting the temperature response of growth

Photoperiod–temperature relationship

Responses to temperature in nature are potentially complicated by species-specific responses to changing photoperiod (review in Corbet, 1999, p. 226). For instance, low temperature may influence the photoperiodic response (Ingram & Jenner, 1976) or fluctuating temperatures may

reduce or even nullify the effect of photoperiod (see below). But we are mainly interested how photoperiod may affect the temperature response. Development of *Epiplatys cynosura* (Say) is generally retarded at 11 hours light compared to 14 hours light, independently of the temperature. With the short photoperiod the developmental rate even decreased with increasing temperature above 20°C. And even at 14 hours light Lutz (1974) did not find major increase in development above 20°C, which is interpreted as photoperiodic inhibition. However, the larvae in this experiment were collected in the field in October and December and may have already been changed to winter metabolism. Interestingly, at naturally fluctuating lake temperatures no photoperiod effect on larvae of *Lestes eurinus* (Say) was notable (Lutz, 1968, figure 3). Moreover, it cannot be excluded that the higher temperature treatments were above the T_{opt} for both species tested by Lutz (1968, 1974). However, a tightly controlled variation of photoperiod demonstrated an increase in developmental rate of *Lestes congener* Hagen (Johansson & Rowe, 1999), although such an increase in developmental rate was not mirrored by an increase in growth rate, a finding confirmed in a study on *Lestes viridis* (Vander Linden) (De Block & Stoks, 2004).

Nonetheless, it seems likely that at least some larval stadia react on photoperiodic cues with reduced or accelerated growth, which has to be considered in studies of TRC. Particularly the temperature response of larvae at or close to winter critical size (Norling, 1984a) will probably be altered by photoperiod. The question is: what are those winter critical sizes? Moreover, it has to be recognized that critical photoperiods are different for populations from different latitudes (Norling, 1984b): larvae of *L. dubia* entered diapause at less than 19 hours light at the polar circle, while they needed 16 hours light in more southerly locations. By contrast, in our experiments young stadium larvae of *L. dubia* from 63°N grew rapidly at only 14 hours light (even more rapidly than those from the southernmost population), which implies that there is probably no major effect on younger stadia. Most of the results compiled in Table 1 are from small larvae reared from the egg under at least 14 hours light; some of the field-sampled larvae were reared under 16 hours light (Supplement 1). Thus, we hope that these results are not or only little affected by photoperiod, although we cannot fully exclude this.

Nutrition: type and availability of food and its assimilation

The second relevant exogenous factor for development besides temperature is the food (i.e. energy) supply. The prey density (Lawton, Thompson, & Thompson, 1980; Wissinger, 1988), the type of prey (Baker, 1986; Hassan, 1976; Johansson, 1993), and the ingestion and assimilation rates (Culler, McPeck, & Ayres, 2014) affect the growth rate, with high amounts and high quality of food allowing rapid growth (Pickup & Thompson, 1990). The study of Hassan (1976) shows clearly how the right type of food affects growth. The duration of larval development (= growth, since there is no diapause) of *Palpopleura lucia* (Drury) varied with the type of prey. At 29°C development from egg until emergence required on average 35.4 days with copepods and cladocerans as food, while it was 42.4 days with mayflies and 46.6 days with ostracods (Hassan, 1976). Thus, the right type of food accelerated growth by 22%. It is obvious that enough food is required for optimal growth and since metabolism speeds up with rising temperature the requirements on food amounts should increase. The functional response depends on temperature due to an increase in attack rate and decrease in handling time. This has been shown in *I. elegans* (Thompson, 1978), *Paragomphus lineatus* (Selys) (Pandian, Mathavan, & Jeyagopal, 1979), and *P. longipennis* (Gresens, Cothran, & Thorp, 1982). In all three studies food intake increased with temperature, in *P. lineatus* up to 35°C. Relative consumption rates, studied in *E. vesperum*, also increased with increasing temperature, while production efficiency showed a unimodal curve similar to the TRC (Culler et al., 2014). Finding the optimal amount and type of food is surely difficult and it cannot be excluded that many of the results compiled in Table 1

may have suffered from too little food, specifically at higher temperatures. This is particularly true when feeding young larvae with *Artemia salina*, as we did, but also many others. The naupliae die in fresh water after some hours and therefore, even if feeding the larvae every day the food supply may not be sufficient. Thus, for future studies it may be necessary to rear *Daphnia* or other more appropriate food.

Do data from fixed temperatures adequately represent growth in nature?

This is an important question but is difficult to answer. Several factors that are tightly controlled in the experiment may vary in the field, such as food availability, biotic interactions (normally not present in TRC experiments) and other density dependent variables. Also the variability of temperature under natural conditions may cause difference in the response (as mentioned for photoperiod response above). We only know a few cases where experiments with fixed temperature and experiments under more natural conditions (cf. McCauley, Hammond, Frances, & Mabry, 2014) were conducted for the same species. From our own studies we have outcomes for both types of conditions for three species. The more natural conditions included naturally varying and partly elevated temperature, natural photoperiod, and biotic interactions – the latter causing changes in density over time. The comparisons did not provide consistent results. For *O. cancellatum* the natural conditions resulted in lower T_{opt} than the fixed ones (Flenner, Richter, & Suhling, 2010; Table 1), indicating that e.g. the competition for food has altered the thermal performance. By contrast, the direct comparisons in *C. erythraea* and *L. dubia* revealed more consistency (Suhling & Suhling, 2013). This gives the hope that simulation models using TRC (cf. Moenickes et al., 2012) will provide useful results – but interpretation has to be careful in all cases and validation with field results is required.

Possible consequences of warming

Dragonflies are warm adapted compared to other aquatic insects. Even the lowest optima are above 20°C and upper thermal limits are also high. Thus, warming in the current distribution ranges should not have many direct harmful effects. Of course, having results for so few species and particularly from only few families, often including many eurytopic species, suffers the risk of biased interpretation. Thus, the main message for evaluating potential effects of climate change is: we need more species-specific information on temperature response. But, maybe some interpretation is permissible. The main processes on the species-level we currently experience are pole-ward range expansions and acceleration in phenology (review in Hassall & Thompson, 2008). These are often assigned to climate warming, in the case of range expansion not necessarily based on mechanistic understanding. We would like to propose one possible mechanism (cf. Soendergerath, Rummland, & Suhling, 2012). The current warming may shift the environmental temperatures towards the optima for growth and, consequently, development may be accelerated. Considering that there is probably a certain mortality risk over time, one may assume that with reduced duration of development the total mortality may also be reduced (less time with mortality risk = less total mortality). This reduction may then allow survival of populations beyond the current range limits, hence shift the distribution range more pole-wards. It may also cause temperature to rise beyond the optimum in distribution ranges nearer the equator, hence slowing development and therefore causing higher total mortality. However, no clear proof exists for range retractions yet. Interestingly, studies using correlative models to forecast the change of distribution ranges with warming predict that the distribution ranges will shrink in many species

(e.g. Bush et al., 2014; Jaeschke, Bittner, Reineking, & Beierkuhnlein, 2012), which at least currently is not evident and for which mechanistic explanation is not always offered. The acceleration in phenology can be easily explained by faster growth (but some species do not respond accordingly, maybe due to seasonal regulation effects; Hassall, Thompson, French, & Harvey, 2007).

There will probably be indirect effects due to biotic interactions. On the one hand, predation risk, for instance by fish, and the response to it may mediate the thermal performance (Culler et al., 2014; cf. Table 1). On the other hand, particularly in odonates we would expect effects within the larval communities mainly due to size mediated predation and priority effects (cf. Rasmussen, Van Allen, & Rudolf, 2014) as well as by the appearance of new community members, i.e. the invasion of pole-wards spreading species. Distinct changes over 10-year periods have indeed been observed in Swedish lake communities (Flenner & Sahlén, 2008) which imply such mechanisms. As shown above generalists and specialists may contrast markedly in the change in growth rate between low and optimal temperatures. For instance, in *L. dubia* the growth rate increased between 16 and 28°C by a factor of three, and in *C. erythraea* by a factor of 10 (Suhling & Suhling, 2013). Such dissimilarity in reaction may alter the phenology of species differently and therefore also the interactions (Yang & Rudolf, 2010). Indeed, experiments showed that the larvae of *C. erythraea* had higher predation effects on *L. dubia* with increasing temperatures (Suhling & Suhling, 2013). A study by Eck, Byrne, Popescu, Harper, and Patrick (2014) indicates that species-specific responses to temperature also affect the predation by different dragonfly species on tadpoles. These examples make clear that a general understanding of climatic impacts on ectothermic populations definitively requires consideration of the community context of thermal physiology (cf. Culler et al., 2014).

Performance of the TRC model

We decided to apply only one function to model TRC for all species as compiled in Table 1. The reason was to make all results directly comparable. But, also the model performance was good. The O'Neill function resulted in all cases in high goodness of fit ($R \geq 0.9$), with only one exception just below that value. Besides that, the O'Neill function directly provided us with two relevant components of the TRC, T_{opt} and Q_{10} , without additional mathematical procedures. Our decision to set a default T_{max} was probably not a perfect solution, but provided meaningful results. But, as pointed out above the model would also allow estimating T_{max} . The question remaining is how to handle T_{min} . One obvious option is again further experiments using many more temperature treatments close to the assumed T_{min} , so around 8–12°C. Dixon et al. (2009) used other models that produce curves cutting through the abscissa, and the cuts at the upper and lower end were defined as T_{min} and T_{max} . But these curves produce negative growth rates, which is appropriate for population growth e.g. of bacteria, but not for size growth in insects. We therefore suggest using the O'Neill model. For further procedures, e.g. use in more complex simulation models, it may be useful to cut-off the curves at a default T_{min} .

Conclusions

The current knowledge of thermal reaction norms of larval growth implies that most odonates are relatively warm adapted, which corroborates the interpretations of Pritchard et al. (1996), who compared egg development of Odonata with that of Plecoptera, Ephemeroptera, and Diptera. This reflects, according to Pritchard et al. (1996), the tropical origin of dragonflies. Also the high

thermal minima and maxima for growth point in this direction. Particularly Libellulidae have high optima for temperature, whereas Coenagrionidae show a wider range. In both families a gradient from more thermally specialized to generalized species occurs, with tropical species tending to higher thermal specialization. But results on TRC are available for very few species and these come from just four families, mainly Coenagrionidae and Libellulidae. Although these are the most species-rich of the 39 families of Odonata, together including more than a third of all described species (Suhling et al., 2015), probably much variation is overlooked. In particular, no families including mainly or exclusively lotic species are represented. Thus, much more species-specific information on temperature response of larval growth is required to draw meaningful conclusions, particularly when aiming prognoses for responses to environmental warming. Also the potential interactions of phenological alterations and competition, predation, and parasitism need more attention. We suggest investigating predation between species possessing different shapes of the TRC.

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Supplemental data

Supplemental data for this article can be accessed via the online version (<http://dx.doi.org/10.1080/13887890.2015.1009392>).

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