Contrasting life-history patterns between vernal pond specialists and hydroperiod generalists in *Lestes* damselflies (Odonata: Lestidae)

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Abstract. The aim of our study was to identify life-history mechanisms enabling typical inhabitants of vernal ponds to complete their larval development under the time constrained conditions of their temporary larval habitats. For that reason we compared both hatching phenology and larval development of vernal pond specialists *Lestes barbarus*, *L. dryas*, and *L. macrostigma* with those of the closely related hydroperiod generalists *L. sponsa*, *L. virens*, and *L. viridis* under seminatural conditions. As hypothesized, we found vernal pond specialists of the genus *Lestes* to cope with the short water coverage of their typical larval habitats by the following developmental traits: a) an early hatching date in *L. dryas* and *L. barbarus*, b) large second-stadium larvae, which have to grow less and with fewer larval stadia than the hydroperiod generalists *L. dryas* and *L. macrostigma*, c) a short larval development time in *L. macrostigma* and d) higher growth rates in *L. dryas* and *L. barbarus* than in the other species. Degree day sums in vernal pond specialists were significantly lower than in their less specialized counterparts. This means, that they would have grown faster than hydroperiod generalists, if thermal conditions during larval development were identical in all species. Due to these developmental adaptations, larvae of *L. dryas* and *L. barbarus* emerged significantly earlier in the course of year than both *L. macrostigma* and the three hydroperiod generalists. Unexpectedly, none of the three studied vernal pond specialists has evolved all of these particular adaptations. This may be because of the close ecological relationship within the genus *Lestes*, and the studied species being generally characterized by univoltine life cycles and fast larval development, which enables all of the European species to reproduce in temporary ponds.

Key words. Dragonfly, damselfly, Zygoptera, hatching phenology, larval development, number of larval stadia

Introduction

Lentic freshwater habitats in temperate regions can be placed along a gradient ranging from small, highly ephemeral puddles to large lakes that have been present for several thousand years (Wellborn et al. 1996).

Along this axis of permanence, temporary ponds »may be defined as bodies of water that experience a recurrent dry phase of varying length that is sometimes predictable in its time of onset and duration« (Williams 1997).

A distinctive type of temporary water are vernal ponds that contain water from late autumn or winter to early summer. Typically, vernal ponds are filled by winter rainfall and/or melt water and desiccate during the summer by evapotranspiration (Williams 2007). According to Williams (1996, 1997), species inhabiting temporary ponds have evolved adaptations permitting their survival. These adaptations can be classified into three types: physiological tolerance, including some form of diapause in the stage surviving the drought, life history modification, and migration. Linked with the loss of water are »the decrease in habitat volume, increase in insolation with subsequent links to water temperature, dissolved oxygen level, primary productivity, pH, and water chemistry« (Williams 1997). As a further consequence of these periodic alterations of water coverage, vernal ponds are usually not inhabited by fish and/or other larger predators (e.g., larvae of semivoltine Odonata species), because the short period during which they contain water does not allow these taxa to complete their life cycles (Williams 1996).

The usability of temporary waters for reproduction is restricted by abiotic conditions, primarily the duration of water coverage. In contrast the distribution of organisms in permanent water is limited largely by biotic factors, especially predation and competition (Wellborn et al. 1996; Williams 1996). It has been demonstrated by Stoks & McPeek (2003a) that both the duration of water cover and the presence or absence of large dragonfly larvae or fish as predators influence the composition of *Lestes* species assemblages in North America.

Within Europe, there are seven *Lestes* Leach, 1815 species (Dijkstra & Lewington 2006), although some authors place *L. parvidens* Artobolevskii, 1929 and *L. viridis* (Vander Linden, 1825) in subgenus *Chalcolestes* Kennedy, 1920 (e.g., Sternberg 1999a; Wildermuth & Martens 2014). Because

our study focuses on life history and developmental aspects of these species, we consider them all *Lestes* for simplicity. All European species of the genus *Lestes*, including *Chalcolestes*, reproduce in shallow water-bodies or shallow parts of larger waters with reed vegetation (reviewed in JÖDICKE 1997). All of them have a rapid univoltine development with nine to 13 larval stadia (JÖDICKE 1997; cf. Table 5), have an egg diapause and over-winter in the egg stage (reviewed in JÖDICKE 1997). Therefore, they can all develop successfully in vernal ponds. However, three of them, *Lestes barbarus* (Fabricius, 1798), *L. dryas* Kirby, 1890, and *L. macrostigma* (Eversmann, 1836), are specialized for this unique type of water body (reviewed in JÖDICKE 1997). Subsequently, we term the specialized species "vernal pond specialists" and the less specialized species "hydroperiod generalists".

To the best of our knowledge no comparative studies on developmental differences between the three vernal pond *Lestes* species and the four hydroperiod generalists have been published hitherto. We hypothesise that in order to face the special demands of their summer-dry larval habitats, the vernal pond specialists *L. barbarus*, *L. dryas*, and *L. macrostigma* hatch earlier in the course of the year. Their second-stadium larvae are expected to be larger, and their larvae should develop faster and with a lower number of larval stadia than the four less specialized congeners *L. parvidens*, *L. sponsa* (Hansemann, 1823), *L. virens* (Charpentier, 1825), and *L. viridis*.

Material and methods

Study sites and egg collection

In 2010, eggs of *L. barbarus*, *L. dryas*, *L. sponsa*, *L. virens*, and *L. viridis* were collected from their oviposition plant tissues in situ (cf. CORBET 1956a; SAWCHYN & CHURCH 1973) at different sites in southwestern Germany, in a range of 47°50'N to 49°11'N (Table 1). Stems of *Bolboschoenus maritimus* containing eggs of *L. macrostigma*, collected in 2009 and 2010 in eastern Austria (Table 1), were provided by courtesy of Theodor Benken. The eggs were kept in the oviposition tissues and placed in plastic boxes with a wet piece of cotton to prevent desiccation. The boxes were stored outside under semi-natural conditions. Rain water was used to prevent accumulation of

Table 1. Sampling sites in southwestern Germany and dates for the collection of eggs of *Lestes* species from their oviposition plant tissues *in situ* for this study. As an exception, *L. macrostigma* eggs were collected by T. Benken in eastern Austria.

Species	Sampling date	Sampling site	Latitude	Longitude	Type of hydroperiod
L. barbarus	06-vii-2010/ 19-ix-2010	pond W of Baden-Baden	48°47′23″N	08°10′51″E	vernal
L. dryas	19-vii-2010	gravel pit SE of Löffingen	47°50′60″N	08°22′33″E	vernal
	05-viii-2010	pond I Freudenstadt	48°27′35″N	08°26′47″E	vernal
L. macro-stigma	01-vii-2009 06-viii-2010	Sechsmahd-lacke, Illmitz	47°47′03″N	16°52′52″E	vernal
L. sponsa	05-viii-2010	pond II Freudenstadt	48°27′24″N	08°26′34″E	permanent
	28-viii-2010	pond W of Achern	48°37′19″N	07°57′18″E	permanent
L. virens	12-ix-2010	gravel pit S of Karlsruhe	48°54′48″N	08°19′53″E	(semi-) permanent
L. viridis	05-xii-2010	gravel pit S of Karlsruhe	48°54′48″N	08°19′53″E	(semi-) permanent

soluble salts. Data on daily average air temperatures were obtained from the nearby weather station of the German Weather Service (DWD) in Rheinau-Memprechtshofen (48°40′N, 07°59′E), which was located about 9 km west of the site where larvae were reared in Sasbach, Baden-Württemberg, Germany (Table 2).

Temperatures and, in consequence, both hatching dates and duration of larval development in natural habitats differ slightly from the semi-natural situation. According to our own occasional measurements, temperatures in the semi-natural conditions were one to two degrees higher than at a pond situated in the open.

Larvae were reared in an unheated room. In this "rearing room", temperatures were more stable, with higher nocturnal lows and lower diurnal highs compared to field conditions. Therefore, the DWD weather station temperature data have to be interpreted with care.

Table 2. Mean air temperatures [°C] during the study period from the DWD weather station at Rheinau-Memprechtshofen (48°40'N, 07°59'E), located close to the study site in southwestern Germany.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
2010	-0.9	2.5	5.9	11.0	12.6	18.6	21.2	18.1	13.8	9.0	6.8	-0.9
2011	2.7	3.9	7.7	13.3	16.2	18.4	17.5	19.5	16.8	10.1	5.5	5.8

Comparison of hatching phenology

On 30-xi-2010, we transferred plant stems containing eggs of *Lestes barbarus*, *L. dryas*, *L. macrostigma*, *L. sponsa*, and *L. virens* in uncovered plastic boxes filled with 400 ml rain water. Twigs with eggs of *L. viridis* were placed in an open bucket with water-covered bottom; the eggs of this species did not get in contact with water. All eggs were kept at outdoor temperature and natural light conditions on an easterly exposed balcony (48°38'N, 08°05'E). The egg containers were kept together in open cardboard boxes placed on the floor. The eggs received no direct sunlight. There was no artificial source of light such as streetlamps disturbing natural photoperiod. However, a possible disturbance of natural photoperiod may have been caused by recording hatching events in the late evening.

The number of freshly hatched larvae was monitored daily, usually in the late evening. During periods with high hatching activity, additional monitoring was carried out in the early morning. The hatchlings were removed from their containers to prevent double counts. In this way, we were able to determine the hatching date of each larva to a precision of one day.

Larval development

Larvae were reared in plastic boxes of volumes ranging between 0.1 and 0.5 l and filled with rain water. The rearing boxes contained pieces of filter paper serving as perching sites. They were placed in an unheated room (48°38'N, 08°05'E) under natural light conditions, provided through windows in the room. Larvae were fed daily *ad libitum* during their complete development. Small larvae were fed with freshly hatched nauplia of *Artemia salina* and later on with *Daphnia* spp. Larger larvae were fed with larvae of Culicidae, Chironomidae, and Chaoboridae.

Table 3. Numbers of hatching events and numbers of larvae of six *Lestes* species analysed concerning various aspects of development. Vernal pond specialists are shaded.

Species		Number of larvae involved in analysis of			
	Hatching events	Number of larval stadia	Duration of larval development	Second stadium larvae measured	F-0 larvae measured
L. barbarus	406	249	271	50	50
L. dryas	242	174	147	50	50
L. macrostigma	12	9	9	12	9
L. sponsa	154	25	24	25	22
L. virens	695	43	43	50	30
L. viridis	10 357	40	40	25	25

We documented the number of larval stadia of each larva and the duration of the complete larval development time (Table 3). Concerning the number of larval stadia we refer to CORBET's (1999: 71) definition, which includes the non-feeding prolarva as the first larval stadium. The prolarva differs morphologically from all following stadia and – although the first larval moult can be postponed for up to 14 hours under unsuitable conditions (reviewed in CORBET 1999: 71) – the prolarval stadium lasts less than one minute in most cases (CORBET 1999: 71). Therefore, we term larvae of the second larval stadium, which succeed the prolarval stadium immediately in our study species, as "second-stadium larvae" (CORBET 2002). The final larval stadium prior to emergence we term F-0 larva *sensu* CORBET (1999, 2002). Data about larval sizes in the following refer either to the second-stadium larvae or to F-0 larvae.

Larvae of each species were kept together in hatching and moult cohorts of a one day precision. Duration between each two moults varied between individuals of an age cohort. Therefore, larvae had to be singularised successively in their containers in order to document the number of larval stadia and development time.

Head width (distance between the outer margins of the eyes) and total length without caudal lamellae of larvae of each stadium were measured one day after each moult using a measuring eyepiece for small larvae and a slide gauge for large larvae. In *Lestes barbarus*, *L. dryas*, and *L. virens* we measured 50 larvae of each stadium, in *L. sponsa* and *L. viridis* 25 larvae of each stadium were measured. We measured all larvae of larger larval stadia when fewer individuals were available. In *L. macrostigma* only 12 larvae were available. Three of them died during development. All individuals were measured (Table 3).

To find out whether there are differences in the development rate of vernal pond specialists *Lestes barbarus*, *L. dryas*, and *L. macrostigma* and the hydroperiod generalists *L. sponsa*, *L. virens*, and *L. viridis*, we compared head width and total length of second-stadium larvae and of F-0 larvae. The quotient of head width of F-0 larvae and head width of second-stadium larvae yielded a "growth coefficient". This expresses how many times the second larval stadia had to multiply their head width until completion of larval development. We also compared growth rates calculated by: (ln[final head width]-ln[initial head width])/(time from hatching until moult in F-0). We determined both growth coefficient and growth rate only for head width, because it is less variable than total length and hence the most reliable measure of overall size in larvae of Odonata (Benke 1970).

Furthermore, we determined the number of larval stadia, the complete duration of larval development from hatching to emergence and the degree day sum per larva. We calculated degree days by summing daily average air temperatures from the DWD weather station (for monthly average temperatures see Table 2) for each larva from hatching to emergence date. The degree day sums calculated with the data of the weather station and those experienced by the larvae in the unheated rearing room differed. Nevertheless, as the temperature conditions in the room changed proportionally to those outside, we consider these data as suitable approximation to compare the degree day sums of the studied species.

Statistical analyses

The software xlstat2014 (Addinsoft 2014) was used for all statistical tests. Since most of the data were not normally distributed, the significance of

all comparisons was tested with non-parametrical two sided Kruskal-Wallis tests, followed by a pairwise comparison using the two sided Mann-Whitney U test with Bonferroni correction. We report original *p*-values.

Results

The hatching phenology of all six *Lestes* species differed significantly (Kruskal-Wallis test among species, p <0.0001). Larvae of the vernal pond specialists, *L. barbarus* and *L. dryas*, hatched significantly earlier (Mann-Whitney U test, *p* <0.0001) than those of the hydroperiod generalists (Fig. 1, Table 4). The third vernal pond specialist, *L. macrostigma*, hatched later than hydroperiod generalist *L. sponsa*, but earlier than *L. virens* and *L. viridis*.

Both head width and total length of second-stadium larvae and of F-0 larvae differed significantly (Kruskal-Wallis test, *p* <0.0001) (Figs 2, 3). Head widths of second-stadium larvae of the vernal pond specialists, *Lestes dryas* and *L. macrostigma*, were significantly larger than those of the other species studied (Mann-Whitney U-test, *p* <0.0001) (Fig. 2). Total length of *L. dryas*
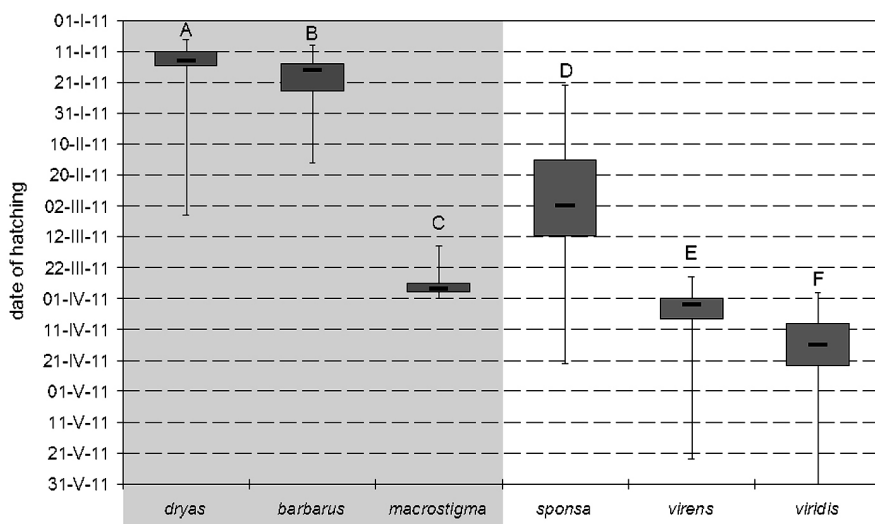

Figure 1. Hatching phenology of all six *Lestes* species in 2011. Boxplots showing maximum and minimum hatching date, quartile 1, 3, and median hatching date. Boxplots identified with different letters differ significantly. Vernal pond specialists are shaded.

second-stadium-larvae was significantly larger than that of all other species (Mann-Whitney U-test, *p* <0.0001). Total length of *L. macrostigma* second-stadium larvae did not differ significantly from that of *L. sponsa*, but was significantly larger than that of *L. barbarus*, *L. virens*, and *L. viridis* (Fig. 2). Second-stadium larvae of the vernal pond specialist *L. barbarus* did not differ significantly from the hydroperiod generalists either in head width or in total length (Fig. 2).

In F-0 larvae, head width of the vernal pond specialist *L. dryas* was significantly larger, and head width of the hydroperiod generalist *L. virens* significantly smaller than that of all other species (Mann-Whitney U-test, *p* <0.0001) (Fig. 3).

In a pairwise comparison, total length of F-0 larvae of the vernal pond specialist *L. dryas* was significantly larger than total length of all other species except for *L. sponsa*, from which it did not differ significantly. Total length of F-0 larvae of the hydroperiod generalist *L. virens* was significantly smaller than total length of all other species (Mann-Whitney U-test,
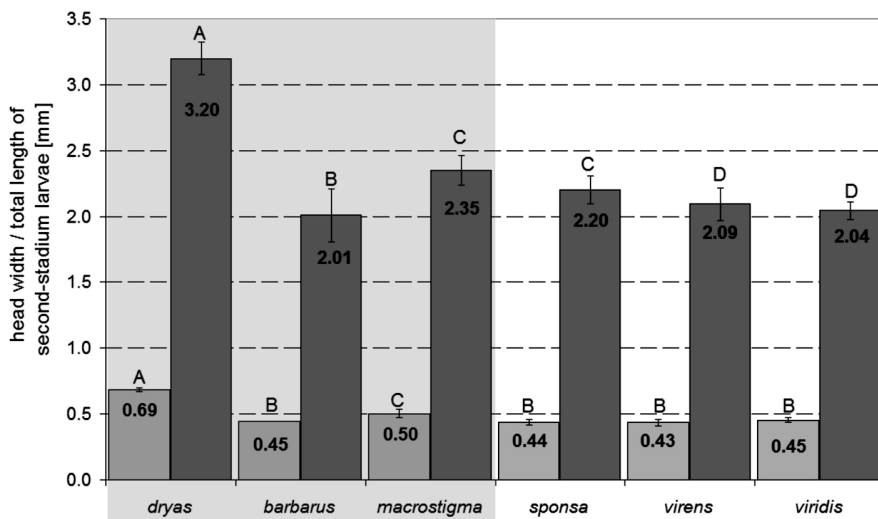

Figure 2. Head width / total length of second-stadium larvae of six *Lestes* species. Bars identified with different letters differ significantly. Vernal pond specialists are shaded.

p <0.0001) (Fig. 3). Total length of F-0 larvae of *L. barbarus* was significantly larger than total length of *L. viridis*, but smaller than that of *L. sponsa*. Total length of F-0 larvae of *L. macrostigma* did not differ significantly from that of *L. viridis* (Mann-Whitney U-test, *p* <0.0001) (Fig. 3).

Second-stadium larvae and F-0 larvae of the vernal pond specialists *L. dryas* and *L. macrostigma* grew less than the other species. Second-stadium larvae of *L. dryas* increased their head width on average 6.1 times, those of *L. macrostigma* 7.7 times. Growth coefficients of the three hydroperiod generalists and of the third vernal pond specialist *L. barbarus* ranged between 8.3 and 9.1 (Fig. 4). Growth coefficients of the vernal pond specialists *L. dryas* and *L. macrostigma* differed significantly from each other and from all other species studied (Mann-Whitney U-test, *p* <0.0001). Furthermore, the growth coefficient of *L. virens* larvae differed significantly from all other species. Growth coefficient of the vernal pond specialist *L. barbarus* was higher than in all other species; it did not differ significantly from growth coefficients of *L. sponsa* and *L. viridis* (Mann-Whitney U-test, *p* <0.0001) (Fig. 4).
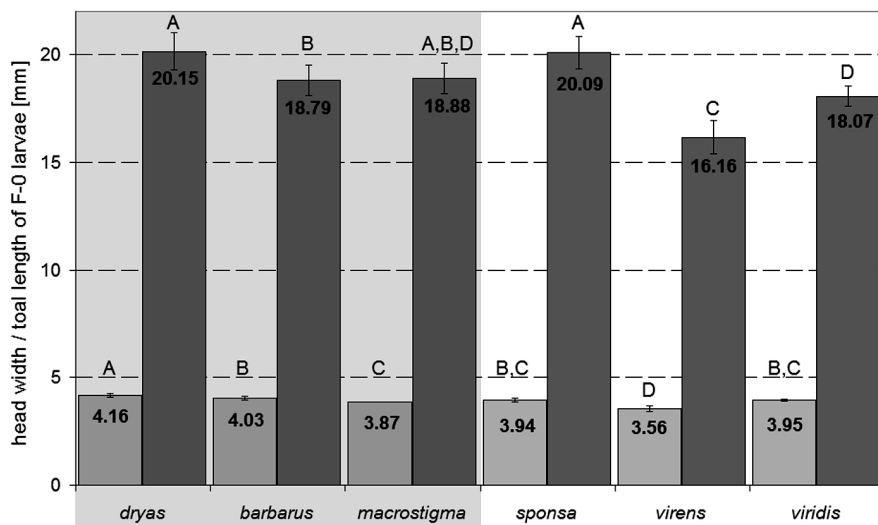

Figure 3. Head width / total length of F-0 larvae of six *Lestes* species. Bars identified with different letters differ significantly. Vernal pond specialists are shaded.

To complete their larval development, the six studied *Lestes* species needed between eight and 12 larval stadia including the prolarva. In our study the number of stadia varied within each species except for *L. viridis*, in which all individuals needed ten stadia to complete larval development. The median number of larval stadia differed significantly among species (Kruskal-Wallis test, *p* <0.0001). Larvae of the vernal pond specialists *L. dryas* and *L. macrostigma* needed significantly less stadia than the other species and also differed significantly from each other (Mann-Whitney U-test, *p* <0.0001). Vernal pond specialist *L. barbarus* needed significantly less stadia than *L. sponsa* and *L. virens*, but did not differ significantly from the hydroperiod generalist *L. viridis* (Mann-Whitney U-test, *p* <0.0001) (Fig. 5).

Complete larval development took between 40 days in one individual of hydroperiod generalist *L. virens* and 105 days in one individual of the vernal pond specialist *L. barbarus*. Medians ranged between 51 days in *L. macrostigma* and 83 days in *L. barbarus* (Fig. 6, Table 6). Median duration of larval development of the six species differed significantly (Kruskal-Wallis test, *p* <0.0001; Fig. 6). Larvae of vernal pond specialist *L. macrostigma*
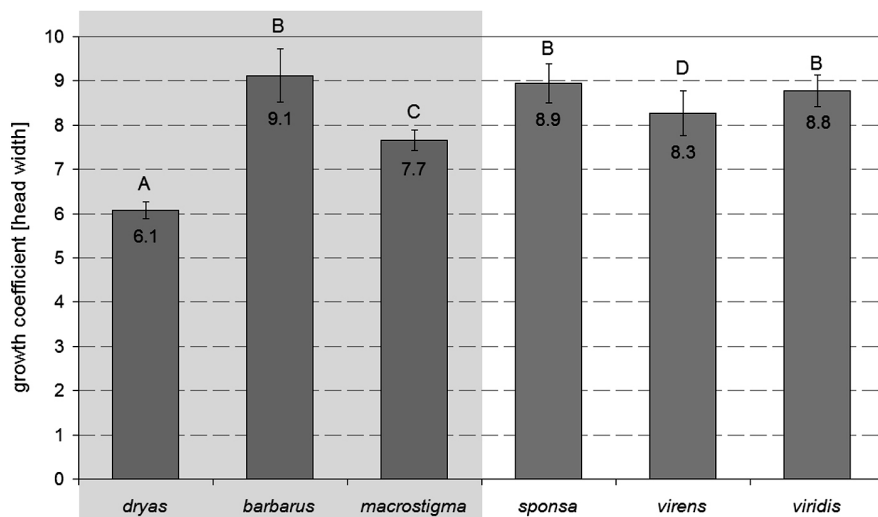

Figure 4. Growth coefficients of six *Lestes* species, calculated by dividing head width of F-0 larvae by that of second-stadium larvae. Bars identified with different letters differ significantly. Vernal pond specialists are shaded.
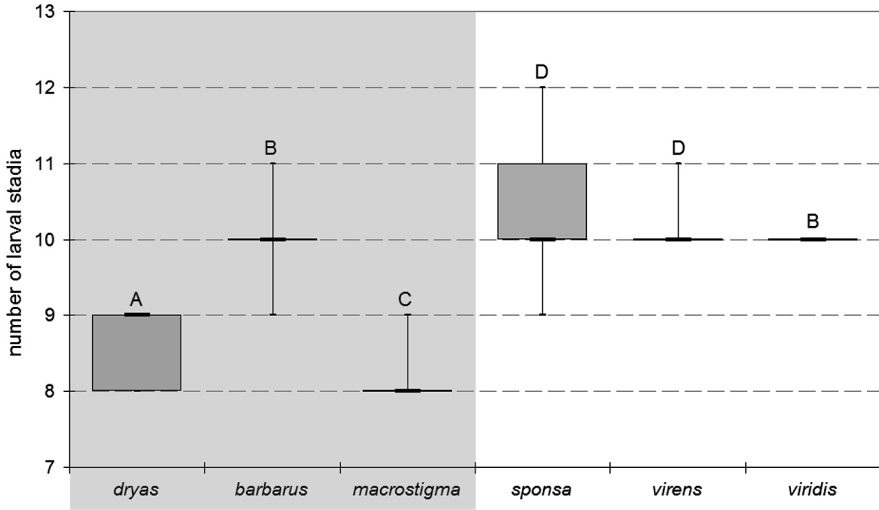
Figure 5. Number of larval stadia of six *Lestes* species. Boxplots identified with different letters differ significantly. Vernal pond specialists are shaded.
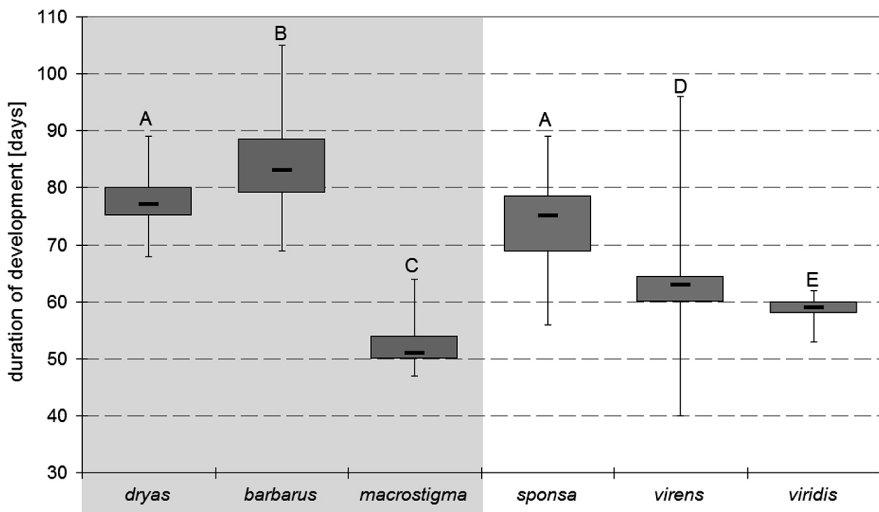

Figure 6. Duration of larval development of six *Lestes* species. Boxplots identified with different letters differ significantly. Vernal pond specialists are shaded.

developed significantly faster than those of all other species (Mann-Whitney U-test, *p* <0.005; Fig. 6). They are followed, in order of development time, by the three hydroperiod generalists *L. viridis*, *L. virens*, and *L. sponsa*. Larvae of vernal pond specialists *L. dryas* and *L. barbarus* had the longest development time. In a pairwise comparison the differences in larval development time among all species were significant except for the difference between median development time of *L. dryas* and *L. sponsa* larvae (Mann-Whitney U-test, *p* <0.005).

Growth rate differed significantly between species (Kruskal-Wallis test, *p* <0.0001). Growth rate of vernal pond specialist *L. dryas* was significantly higher, and that of hydroperiod generalist *L. virens* was significantly lower than those of all other species (Mann-Whitney U-test, *p* <0.0001) (Fig. 7). *Lestes barbarus* had the second highest growth rate followed by that of *L. viridis*, *L. sponsa*, *L. macrostigma*, and *L. virens* (Fig. 7). In a pairwise comparison the growth rates of *L. barbarus* and *L. viridis* and those of *L. viridis*, *L. sponsa*, and *L. macrostigma* did not differ significantly (Mann-Whitney U-test, *p* >0.005).
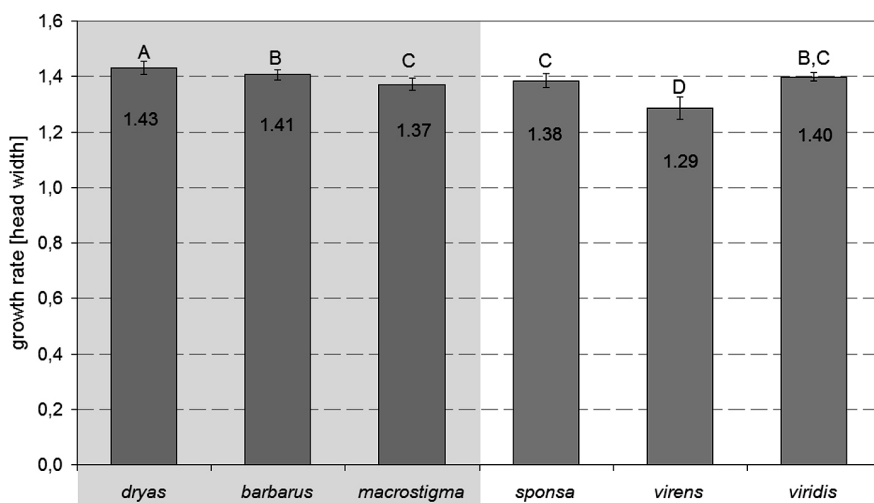

Figure 7. Growth rates of six *Lestes* species. Bars identified with different letters differ significantly. Vernal pond specialists are shaded.

To take temperatures during larval development into account, we expressed development in degree day sums per larva. This resulted in a different order among the species. Median degree day sums ranged between 411.5 in *L. dryas* and 915.6 in *L. virens* (Fig. 8). Median degree day sums of the six species differed significantly (Kruskal-Wallis test, *p* <0.0001; Fig. 8). Larvae of the vernal pond specialists *L. dryas* and *L. barbarus* had significant lower degree day sums than all other species and also differed significantly from each other (Mann-Whitney U-test, *p* <0.005; Fig. 8). They are followed, in order of degree day sums, by the vernal pond specialist *L. macrostigma* and the three hydroperiod generalists *L. sponsa, L. viridis*, and *L. virens*.

Vernal pond specialists *L. dryas* and *L. barbarus* completed larval development first followed by – in order of emergence – hydroperiod generalist *L. sponsa*, vernal pond specialist *L. macrostigma*, and hydroperiod generalists *L. virens* and *L. viridis* (Fig. 9). The differences in median emergence date of the six species were significant (Kruskal-Wallis test, *p* <0.0001). In a pairwise comparison all differences except that between *L. macrostigma* and *L. sponsa* were significant (Mann-Whitney U-test, *p* <0.005).
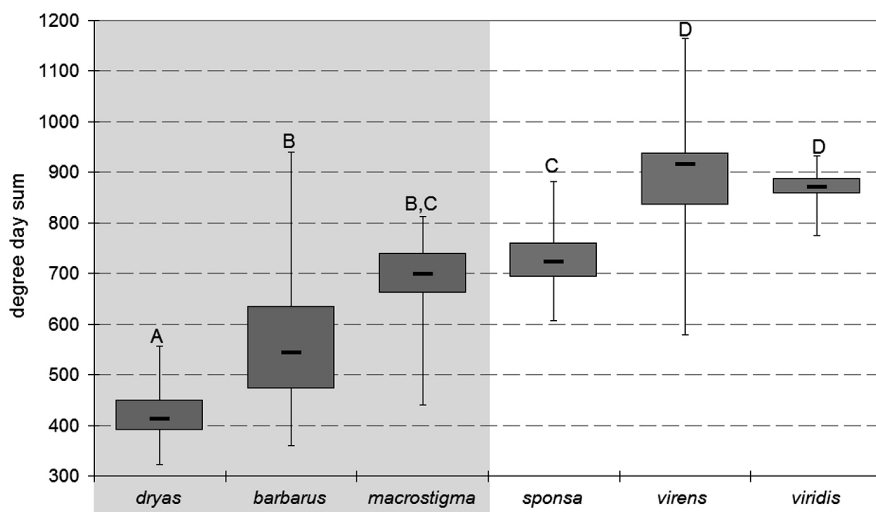

Figure 8. Degree day sums of six *Lestes* species. Boxplots identified with different letters differ significantly. Vernal pond specialists are shaded.

Discussion

In our study we aimed to find out if there are developmental differences between larvae of Odonata species ecologically specialized in vernal ponds and less specialized congeners reproducing both in temporary and permanent water bodies.

Vernal ponds are a distinctive type of temporary wetland typically filled by winter rains and/or melt water and drying out in the course of summer; therefore vernal ponds are usually free of large predators such as fish or larger dragonfly larvae (Stoks & McPeek 2003a; Wellborn et al. 1996;
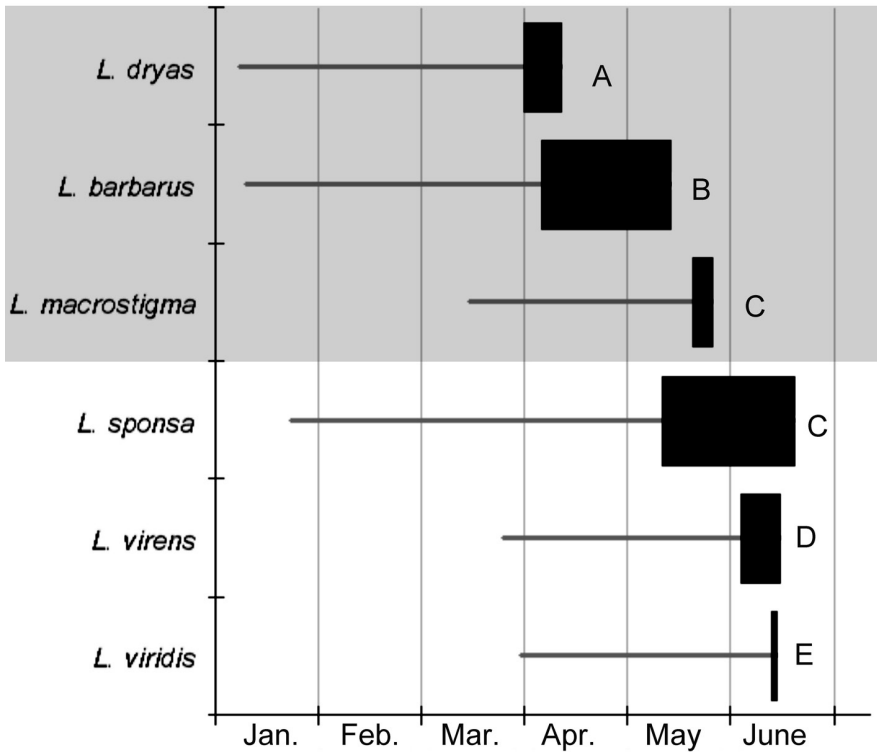

Figure 9. Emergence phenology of all six *Lestes* species in 2011 by combining hatching phenology with larval development time. The lines represent the larval development time from hatching to start of emergence, the bars the complete emergence period. Data identified with different letters differ significantly. Vernal pond specialists are shaded.

Williams 2007). Therefore, reproduction in vernal ponds may be a strategy to avoid competition with and predation by congeners and other predators developing in semi-permanent or permanent waters (Wellborn et al. 1996; Stoks & McPeek 2003a; Williams 2007). In vernal pond specialists, the avoidance or at least reduction of predation and competition by other species apparently outweighs the great disadvantage that duration of water coverage is restricted. Next to behavioural adaptations like a fast and open life style (Johansson & Suhling 2004) and physiological traits like a higher digestive efficiency (Stoks & McPeek 2003b) this specialization has implications for life history (Wellborn et al. 1996; Stoks & McPeek 2003a; Williams 2007). To cope with the risk of early drying-up of the larval habitats, specialized species should be adapted by both early hatching and shortened larval development.

Concerning early hatching, our results support the hypothesis for vernal pond specialists *L. barbarus* and *L. dryas*, whereas *L. macrostigma* hatched at an intermediate period significantly earlier than hydroperiod generalists *L. virens* and *L. viridis*, but significantly later than the two other vernal pond specialists and than hydroperiod generalist *L. sponsa* (Table 4). Early hatching has already been demonstrated to be a strategy in temporary pond populations of *L. viridis* (De Block & Stoks 2004, 2005a; De Block et al. 2005). It has also been shown in a comparative study on 15 European species including typical vernal pond specialists *Aeshna affinis* Vander Linden, 1820 and *Sympetrum flaveolum* (Linnaeus, 1758) (Schiel & Buchwald 2015). In a pond in Latium, Italy, *L. barbarus* hatched two months earlier than coexisting *L. virens* (Carchini & Nicolai 1984). In Canadian populations of *L. dryas*, early hatching in comparison with populations of *L. unguiculatus* Hagen, 1861 and *L. disjunctus* Selys, 1862 was suspected by Sawchyn & Gillott (1974a).

To protect the supposed cold-sensitive early larval stadia of univoltine *Lestes* species (Corbet 1999) from unfavourable low winter temperatures and to survive drought phases in the larval habitats (Williams 1996) many of these species exhibit delayed development with egg diapause, which is regarded as a special type of physiological adaptation (Williams 1996, 1997); egg diapause can be terminated by water contact (e.g., Sawchyn & Gillot 1974b, for *Lestes congener*) and controlled by temperature (e.g., Münch-

Table 4. Overview of published hatching dates of the investigated *Lestes* species, compared with the data of this study. Based on Table 24 in JÖDICKE (1997). In the columns "Data from this study" and "Literature", months without brackets represent the hatching span between quartile 1 and 3, months in brackets represent minimum and maximum hatching data observed, which may be not typical or artefact. Vernal pond specialists are shaded.

Species	Data from this study	Literature	Sources
L. barbarus	January (to February)	(October to December), (January) February to April	LOIBL (1958); AGUESSE (1961); CARCHINI & NICOLAI (1984); ROTA & CARCHINI (1988)
L. dryas	January (to March)	(November) March / April	NEEDHAM (1903); WESENBERG-LUND (1913); GARDNER (1952); SAWCHYN & CHURCH (1973)
L. macro-stigma	March	no data available	JÖDICKE (1997)
L. sponsa	February / March (January to April)	(September, October to December), April to June	WESENBERG-LUND (1913); MÜNCHBERG (1933); CORBET (1956b); LOIBL (1958); ŚNIEGULA & JOHANSSON (2010)
L. virens	(March) first decade of April to May	(October) April to End of May	MÜNCHBERG (1933); CARCHINI & NIKOLAI (1984); ROTA & CARCHINI (1988)
L. viridis	(March) mid-April to May	Beginning of April to mid-June	MÜNCHBERG (1933); LOIBL (1958); STERNBERG (1999a); DE BLOCK et al. (2005a)

BERG 1933; CORBET 1956a, for *L. sponsa*), and photoperiod (e.g., SAWCHYN & CHURCH 1973, for *L. disjunctus* and *L. unguiculatus*; ŚNIEGULA & JOHANSSON 2010, for *L. sponsa*). The influence of day length in triggering hatching has already been shown for *L. disjunctus*, *L. unguiculatus*, and *L. dryas* in Canada (SAWCHYN & CHURCH 1973) and for *L. sponsa* in Europe (ŚNIEGULA & JOHANSSON 2010). The latter species hatched earlier in longer photoperiods, which is typical for higher latitudes (ŚNIEGULA & JOHANSSON 2010).

In addition to early hatching, fast larval development should be an appropriate adaptation facing drought in immature water insects. Fast larval development includes physiological, behavioural, and morphological aspects (WILLIAMS 1996, 1997). In our study we focussed on size and development

time. Among other traits, fast development may be optimised by large larval size at hatching and a comparatively small size difference between second-stadium larvae and F-0 larvae. This would enable development with fewer larval stadia and within a shorter time span.

Indeed, head widths of second-stadium larvae of vernal pond specialists *Lestes dryas* and *L. macrostigma* were significantly larger than those of other species studied, and both size differences between second-stadium larvae and F-0 larvae and number of larval stadia were smaller in these two species than in hydroperiod generalists and in the third vernal pond specialist, *L. barbarus*.

According to our data, *L. sponsa* needed up to one, *L. barbarus* up to two, and *L. dryas* between two and five stadia less than has been documented in previous studies (for references see Table 5). *Lestes viridis* was the only species in which the number of larval stadia was within the range of former studies (Table 5). To the best of our knowledge, the number of larval stadia of *L. macrostigma* and of *L. virens* was unknown hitherto (Jödicke 1997, Table 5). With eight to nine larval stadia, *L. macrostigma* is at the lower end and *L. virens*, with 10–11 larval stadia, in the center of the known span of larval stadia in *Lestes* (Fig. 5, Table 5).

Growth rate and larval development time are influenced by environmental factors like photoperiod (e.g., Norling 1984a, 1984b; De Block & Stoks 2004, 2005b; Śniegula & Johansson 2010; Śniegula et al. 2012, 2014), temperature (e.g., Pickup & Thompson 1984; Krishnaraj & Pritchard 1995; De Block & Stoks 2003), food availability (e.g., Fischer 1972; Pickup & Thompson 1984; Johansson et al. 2001), and larval densities (De Block & Stoks 2005a). Differences in these variables may have contributed to the different results concerning number of larval stadia (Table 5) and duration of larval development (Table 6). This demonstrates high developmental plasticity in all species (reviewed in Stoks et al. 2008). In our study only photoperiod and temperature changed according to natural conditions. Larvae that hatch later experience inherently longer photoperiods and higher water temperatures.

Larvae of the vernal pond specialists *L. dryas* and *L. macrostigma* needed only eight to nine larval stadia. This was a significantly lower number of larval stadia than in all other species including the third vernal pond

Table 5. Overview on published data about the number of larval stadia (counting the prolarva as stadium 1) of the investigated *Lestes* species, compared with the data from this study. Vernal pond specialists are shaded.

Species	Number of larval stadia	Sources	Data from this study
L. barbarus	11–12	LOIBL (1958)	9–11 (12)
	12	AGUESSE (1961)	
L. dryas	11	GARDNER (1952)	8–9
	12–13	FISCHER (1964)	
L. macrostigma	unknown		8–9
L. sponsa	10–12	LOIBL (1958)	9–12
	13	MÜNCHBERG (1933); FISCHER (1959)	
L. virens	unknown		10–11
L. viridis	9–10	LOIBL (1958)	10
	10	PRENN (1927); ROBERT (1959)	
	10–11	GEIJSKES (1928)	
	13	MÜNCHBERG (1933)	

specialist *L. barbarus*, which needed nine to eleven stadia in our study. The latter needed significantly less stadia than *L. sponsa* and *L. virens*, but did not differ significantly from the hydroperiod generalist *L. viridis* (Fig. 5).

According to an analysis comprising 85 Odonata species from 47 genera and 11 families, the number of larval stadia, including the prolarva, ranges generally from 8 to 17 with a median of twelve stadia (CORBET 1999: 208). Of the analysed species, 63 % needed 11 to 13, 86 % 10 to 14, and 96 % nine to 15 stadia (CORBET 1999: 208). The number of larval stadia in European *Lestes* species generally ranges between nine and 13 stadia (reviewed in JÖDICKE 1997). Therefore, number of larval stadia in the genus *Lestes* is towards the lower end of the range needed to complete larval development. In *L. dryas* and *L. macrostigma* the number of larval stadia even falls outside the widest range.

In our rearing study *L. macrostigma* was the only vernal pond specialist, which developed significantly faster than its less specialized congeners.

Unexpectedly, the vernal pond specialists *L. barbarus* and *L. dryas* had the longest development time among all studied *Lestes* species and developed significantly slower than hydroperiod generalists *L. virens* and *L. viridis*. This paradox may be explained by differences of temperature and photoperiod. From experiments conducted by Krishnaraj & Pritchard (1995) on *Coenagrion resolutum* (Hagen *in* Selys, 1876) and *L. disjunctus* it can be assumed that obligatory univoltine *Lestes* species have a higher thermal coefficient than non-obligatory univoltine summer species like *C. resolutum*. In our study the late-hatching hydroperiod generalists may have reacted to the higher temperatures at this later time of year by accelerating their growth rate and developing faster than their vernal pond congeners, which had hatched earlier in the course of the year when temperatures were lower. This explanation is supported by our analysis of degree day sums (Fig. 8). Furthermore it has been demonstrated in several studies (e.g., Strobbe & Stoks 2004; De Block & Stoks 2004, 2005a, b) that late-hatching larvae are capable of growing and developing faster under photoperiodically regulated time constraints than larvae of the same species that hatched earlier in the course of the year. According to Stoks et al. (2008), without time constraints damselfly larvae may not make use of their growth and development potential to reduce their risk of starvation (De Block & Stoks 2004) or predation (Stoks et al. 2005).

This regulation may also have resulted in the unexpected faster development of hydroperiod generalist species compared to the vernal pond specialists *L. barbarus* and *L. dryas*. Nevertheless, the vernal pond specialists *L. barbarus* and *L. dryas* completed larval development significantly earlier than all other species in our study due to their early hatching date. In fact, in our study both *L. barbarus* and *L. dryas* emerged more than one month earlier than under natural conditions in these latitudes (Hunger et al. 2006). This may have been caused primarily by the very early hatching dates, because larval development time span tended to be longer in our study than in other studies (Table 6).

According to Corbet (1962, 2003) there are three different types of life cycles in Odonata in temperate latitudes. Species of the genus *Lestes* belong to a small subset of summer species that overwinter in (usually) obligate egg diapause and are obligatorily univoltine and develop in 2–3 months in

Table 6. Selection of exemplary studies about total development time of the investigated *Lestes* species, compared with data from this study. Vernal pond specialists are shaded.

Species	Minimum time span of larval development [d]	Sources	Median development time span in this study [d] (total time span)
L. barbarus	~ 30 (?) ~ 46–60 ~ 90	SCHMIDT (1990) AGUESSE (1961) CARCHINI & NICOLAI (1984)	83 (69–105)
L. dryas	43–46 45 ~ 60–74 195	DE BLOCK et al. (2007, 2008) ROBERT (1959) SCHIEMENZ (1953) GARDNER (1952)	77 (68–89)
L. macro-stigma	~ 56–70	WILDERMUTH & MARTENS (2014)	51 (47–64)
L. sponsa	37 42 42–60 50–64 71 68–83 ~ 100	SCHMIDT (1993) WESENBERG-LUND (1913); CLAUSNITZER (1974) LOIBL (1958) ŚNIEGULA & JOHANNSON (2010) CORBET (1956b) PICKUP et al. (1984) JOHANSSON et al. (2001)	75 (56–89)
L. virens	~ 60–90	CARCHINI & NICOLAI (1984)	61 (40–96)
L. viridis	48–62 61 62 62–67 65–70 106	LOIBL (1958) ROLFF et al. (2004) DE BLOCK & STOKS (2005a, b) PRENN (1927) MÜNCHBERG (1933) ROBERT (1959)	59 (53–62)

spring and early summer. Their obligatory univoltine life cycle (CORBET et al. 2005), with fast larval development and egg diapause, may serve to protect temperature sensitive early larval stadia from winter cold (CORBET

1999), but is a good pre-adaptation to colonize vernal ponds, where the genus is well represented (reviewed by Jödicke 1997). In fact, De Block et al. (2007) concluded that vernal pond inhabitants of the genus *Lestes,* such as *L. dryas,* have evolved from ancestral species, which reproduced in temporary waters. Compared with *L. barbarus* and *L. macrostigma*, *L. dryas* shows more developmental adaptations for successful reproduction in vernal ponds. This might be correlated with its high latitudinal range (reviewed by Jödicke 1997). In comparison with both of its more southerly distributed vernal pond congeners (reviewed by Jödicke 1997) some populations of *L. dryas* are not only time-constrained by drying up of larval habitats, but may also experience lower temperature sums in their larval habitats due to harsher climate conditions in higher latitudes.

As hypothesized, the following developmental traits are put into effect in typical vernal pond specialists of the genus *Lestes*: a) an early hatching date in *L. barbarus* and *L. dryas*, b) large second-stadium larvae in *L. dryas* and *L. macrostigma*, which have to grow less and with fewer larval stadia than permanent pond congeners, c) a very short larval development time in *L. macrostigma,* and d) highest growth rates in *L. dryas* and *L. barbarus*. Degree day sums in vernal pond specialists were significantly lower than in their less specialized counterparts. Unexpectedly, none of the three studied vernal pond specialists has evolved all of these particular adaptations. This may be caused by the close ecological relationship within the genus *Lestes*, with all studied species being characterized by univoltine life cycles and fast larval development, which enables all of the European species to reproduce in vernal ponds (e.g., Jödicke 1997; Röhn et al. 1999; Sternberg 1999a, b; Sternberg & Röske 1999; Wildermuth & Martens 2014).

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