How to survive the brief water-coverage of vernal ponds?
Early hatching date and rapid larval development in *Aeshna affinis* (Odonata: Aeshnidae)

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Abstract. The objective of our study was to identify mechanisms enabling typical inhabitants of vernal ponds in temperate climate zones to complete their larval development under the time-constrained conditions of temporary larval habitats. We compared both hatching phenology and larval development of *Aeshna affinis* with those of its permanent water congener *A. mixta* under semi-natural conditions and with literature data on other European Aeshnidae. We identified the following traits enabling rapid univoltine development in vernal ponds: i) Seasonally early hatching: *A. affinis* hatched significantly – on average 22 days – earlier than *A. mixta*. ii) Relatively small size difference between the second and the final larval stadium: Second-stadium larvae of *A. affinis* were significantly larger than those of all other European Aeshnidae, but the exuviae are among the smallest of this family in Europe. Therefore, larval growth coefficient and the number of larval stadia are smaller than in any other European Aeshnidae. iii) A low degree-day sum during larval development, being significantly lower than that of *A. mixta*. Although median larval development time of the vernal pond species *A. affinis* was longer than that of *A. mixta*, the first emerged significantly – on average 18 days – earlier than the latter.

Further key words. Dragonfly, Anisoptera, hydroperiod, life history, hatching phenology, time constraints

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).

The life cycles of organisms inhabiting temporary waters are mainly influenced by the duration and pattern of water appearance. 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 periodical alterations of water coverage, vernal ponds are usually not inhabited by fish and/or other large predators, because the short hydroperiod does not allow these species to complete their life cycles (Williams 1996).

Aeshna affinis Vander Linden, 1820 is a characteristic inhabitant of summer-dry temporary waters – vernal ponds – (e.g., Bernard & Samoląg 1997; Sternberg et al. 2000; Brauner 2005), which are typically filled by winter rainfall or snowmelt and desiccate during the summer by evapotranspiration (Williams 2007). With regard to this specific habitat preference, *A. affinis* differs from all other European representatives of the Aeshnidae. The species has a huge range reaching from the Iberian Peninsula and north-western Africa to Central Asia (Schröter 2011; Kalkman & Dyatlova 2015). The number of populations and the abundances seem to increase from West to East, with huge populations at some sites of Central Asia (Schröter 2011). Therefore, the species seems to be adapted to continental climate.

In the last two decades, *A. affinis* has presumably expanded its range as a consequence of climate warming in Europe (e.g., Ott 2000). For that reason the species has been subject to a series of faunistic publications (e.g., Adomssent 1995; Martens & Gasse 1995; Schiel & Kunz 2005; Schröter & Karjalainen 2009). However, only a few authors have dealt with its habitat requirements (Brauner 2005; Schröter 2011) or life cycle (Bernard & Samoląg 1997).

In general, voltinism and duration of larval development in the Odonata are difficult to determine. Both can be identified by analysis of larval population structure (e.g., Müller et al. 2000; Leipelt et al. 2001; Mikolajewski et al. 2004) or by systematically collecting exuviae at newly created

waters bodies (e.g., Martens 1986; Weisheit 1995; Burbach 2000; Koch 2003; Schiel 2006; Schirrmacher et al. 2007). A third method, which is the most precise identifing the number of larval stadia, is rearing larvae under laboratory conditions from hatching to emergence (e.g., Robert 1959; Sternberg 1990; Grunert 1995).

In order to survive the specific demands of their summer dry larval habitats, larvae of *A. affinis* are expected to be adapted by seasonally early hatching (e.g., De Block et al. 2005, for *Chalcolestes viridis* (Vander Linden, 1825); Schiel & Buchwald 2015a, for several species) and rapid larval development (e.g., Johansson & Suhling 2004; Suhling et al. 2004; Schiel & Buchwald 2015b). In both aspects, we predict that it differs from its closest Eurasian relative, *A. mixta* Latreille, 1805 (Peters 1987). Furthermore, second stadium larvae of *A. affinis* are expected to be larger and its larvae should develop with a lower number of larval stadia than those of *A. mixta* (e.g., Schiel & Buchwald 2015b, for several *Lestes* species). We tested these hypotheses by comparing the hatching phenology and larval development of the vernal pond specialist *A. affinis* with that of the closely related permanent pond species *A. mixta* under semi-natural conditions.

Material and methods

Definitions

Corbet (1999: 207) distinguishes the terms 'instar' and 'stadium'. Following his definition (Corbet 1999: 207), the instar begins with apolysis – »the moment when a new layer of cuticle is laid down inside the old one«. The term 'stadium' means the period between two moults. Because we were only able to determine the intermoult interval, we subsequently use this term.

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 species (Corbet 1999: 71). Therefore, we term larvae of the second larval stadium, which succeeded the prolarval stadium immediately in our study species, as 'second-stadium larvae'.

Table 1. Sampling sites in the Upper Rhine valley, Baden-Württemberg, Germany, and sampling dates of *Aeshna affinis* and *A. mixta* females.

Species	Sampling dates	Sampling site	Latitude [N]	Longitude [E]	Type of hydroperiod
Aeshna affinis	08-viii-2008 14-viii-2008 21-viii-2008	Ponds S of Ubstadt	49°09′12′′	08°37′02′′	vernal
Aeshna mixta	14-viii-2008	Ponds S of Ubstadt	49°09′12′′	08°37′02′′	vernal
	20-viii-2008 21-viii-2008	Gravel pit S of Karlsruhe	48°54′46′′	08°19′52′′	(semi) permanent
	30-viii-2008 21-ix-2008	Gravel pit SW of Baden-Baden	48°46′33′′	08°02′01′′	(semi) permanent
	28-ix-2008	Oxbow Breisach	48°05′12′′	07°34′30′′	permanent

Study sites and egg collection

The study was carried out in 2008 and 2009. Between 08-viii-2008 and 28-ix--2008, nine females of *Aeshna affinis* and eight females of *A. mixta* had been forced to oviposit in captivity into tissue paper. The females originated from different sites in the Upper Rhine valley, Baden-Württemberg, Germany, in a range between 48°05′N and 49°09′N (Table 1). We kept the eggs in the oviposition tissues placed in plastic boxes with a moist piece of cotton to prevent desiccation. The boxes were stored outside under semi-natural conditions. We used exclusively rainwater to prevent accumulation of soluble salts.

Comparison of hatching phenology

On 30-xi-2008, we transferred half of the eggs of each female into closed Petri dishes filled with 30 ml rainwater. We kept all eggs 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 boxes placed on the floor. The eggs were not exposed to direct sunlight. There was no artificial source of light such as street lamps disturbing natural photoperiod. We monitored the number of freshly hatched larvae daily, usually in the late evening. During periods of high hatching activity, we carried out additional

Table 2. Mean air temperatures [°C] during the study year 2009 at the DWD weather station Rheinau-Memprechtshofen, Germany (48°40'N, 07°59'E), situated next to the study site where *Aeshna affinis* and *A. mixta* larvae were bred.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
2009	-2.0	1.8	5.8	12.6	15.9	17.6	19.3	19.9	15.9	9.8	8.5	3.0

monitoring in the early morning. We removed freshly hatched larvae 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. These data were analysed to compare interspecific differences in hatching date.

Data on daily average air temperatures were obtained from the nearby weather station of the 'Deutscher Wetterdienst' (DWD) in Rheinau-Memprechtshofen (48°40'N, 07°59'E), which is located about 9 km west of the study site (Table 2).

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

Larval development
Larvae were raised in rainwater-filled plastic boxes of volumes ranging between 0.1 and 0.5 l depending on number of larvae per cohort and larval sizes. Larvae originating from different clutches were mixed in each container. 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 development. Small larvae of the second stadium were fed with freshly hatched nauplia of *Artemia salina*. From third to fourth stadium they got *Daphnia* spp. and larger larvae from fifth to sixth stadium were fed with larvae of Culicidae, Chironomidae, and Chaoboridae until emergence.

In *A. affinis* we documented the number of larval stadia of each larva and the duration of larval development. Larvae of *A. affinis* were kept together in

hatching and moult cohorts. Duration between each moult varied between individuals of a single hatching cohort. Therefore, larvae were isolated 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 of 50 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 *A. mixta* we only documented the total development time and measured head width and total length of 50 second-stadium larvae and 50 exuviae.

To find out whether there were differences in the development time of *A. affinis* and the closely related *A. mixta*, we compared head width and total length of second-stadium larvae and of exuviae. The quotient of head width of exuviae and head width of second-stadium larvae yielded a 'growth coefficient'. We also compared growth rates in *A. affinis* and *A. mixta* calculated by following formula: [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). For comparison, we calculated growth coefficients of other European Aeshnidae where data of head widths of second-stadium larvae were available. We did this for each species by dividing average head width of ten exuviae (from our own collection) with head width of second stadium larvae from literature. We presuppose that these literature data are sufficiently precise for our interspecific comparison although size of second stadium larvae may vary across populations (e.g., Śniegula et al. 2016, for *Lestes sponsa*). In *A. affinis* we also determined the growth coefficient for successive larval stadia.

Finally, we determined degree-day sums for the complete larval development time in *A. affinis* and *A. mixta*. Degree-days are defined as the total amount of heat required for an organism to develop from one point to another in its life cycle (Baskerville & Emin 1969).

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 weather station data and those experienced by larvae in the unheated

rearing room differed. Nevertheless, as temperature conditions in the room changed according to those outside, we consider these data as suitable approximations to compare the degree-day sums of the two studied species.

Statistical analyses

The software xlstat2014 (Addinsoft 2014) was used for all statistical tests. Since most data were not normally distributed, we tested significance of all comparisons with the non-parametrical, two sided Mann-Whitney U test.

Results

In total, we documented 855 hatching events of *Aeshna affinis* and 681 of *A. mixta*. Larvae of *A. affinis* hatched significantly earlier than those of *A. mixta* (U = 555 993, $p < 0.0001$; Fig. 1). Median hatching date of the first species was 16-iii-2009, that of the latter species 07-iv-2009.

In 142 larvae of *A. affinis* the number and duration of larval stadia was documented. To complete its larval development, *A. affinis* needed between nine and ten larval stadia including the prolarva. In total, 40 (28 %) individuals needed nine and 102 (72 %) individuals ten stadia (Figs 2, 3; Table 3). In *A. affinis* larval intermoult stadia took on average between seven and eleven days with a median of nine days (Fig. 2). The period between final larval moult and emergence lasted on average 25 days. Time span of this last intermoult stadium did not differ significantly among larvae that needed nine and those that needed ten larval stadia (U = 2 196.5, $p = 0.472$) (Fig. 2). Larvae grew steadily throughout their development (Fig. 3). Concerning head width, median growth coefficient between each two stadia averaged 1.26, ranging between 1.21 and 1.4. From final larval moult to emergence, larvae grew very little: median growth coefficient totalled 1.0 in head width and 1.04 in total length (Fig. 3).

Both head width and total length of second-stadium larvae of *A. affinis* were significantly larger than those of *A. mixta* (U head width = 2 489, U total length = 2 537, $p < 0.0001$) (Fig. 4). In exuviae, head width of *A. affinis* was significantly larger than that of *A. mixta* (U = 3 023, $p = 0.035$); total length did not differ significantly between these two species (U = 2 249.5, $p > 0.317$) (Fig. 5).
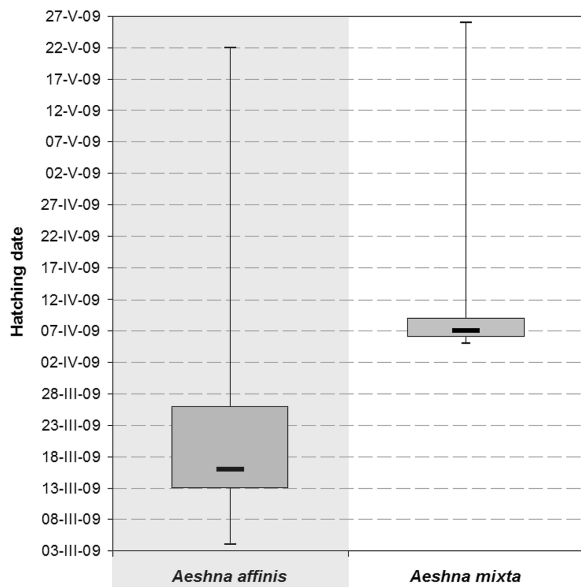
Figure 1. Hatching phenology of *Aeshna affinis* and *A. mixta* in 2009 of eggs laid by females originating from different sites in the Upper Rhine valley, Baden-Württemberg, Germany, under semi-natural conditions. Boxplots show maximum and minimum hatching date, quartile 1, 3, and median hatching date.
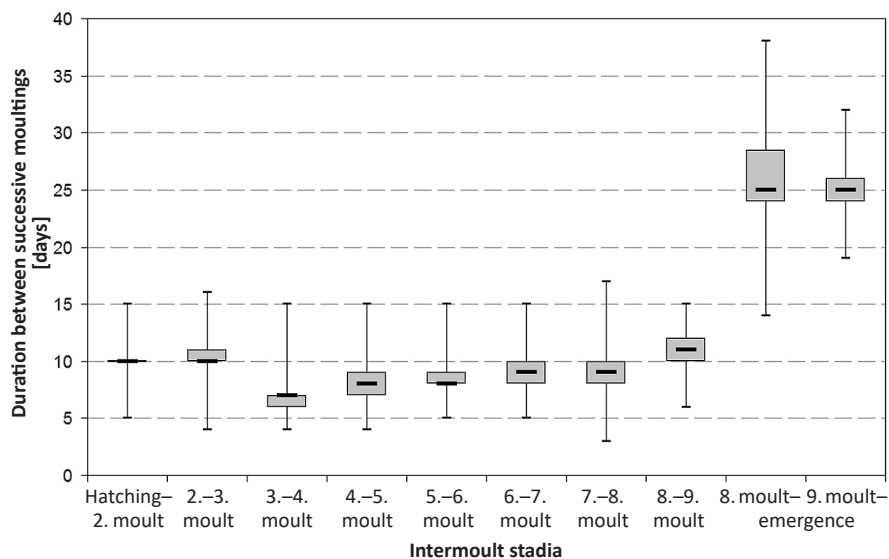

Figure 2. Duration of intermoult stadia in *Aeshna affinis*. Boxplots show maximum and minimum, quartile 1, 3, and median number of days between each two successive moultings.
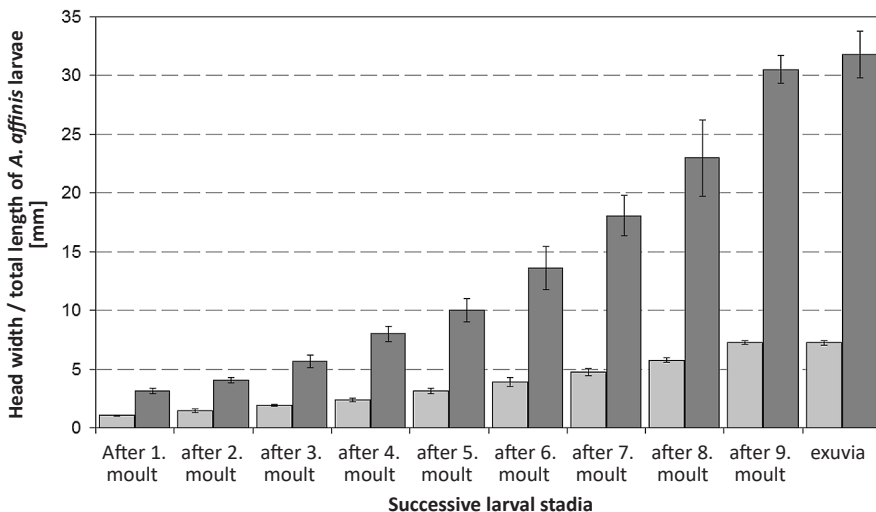
Figure 3. Size increase in successive larval stadia of *Aeshna affinis*. Bars in light grey represent head width, those in dark grey total length.
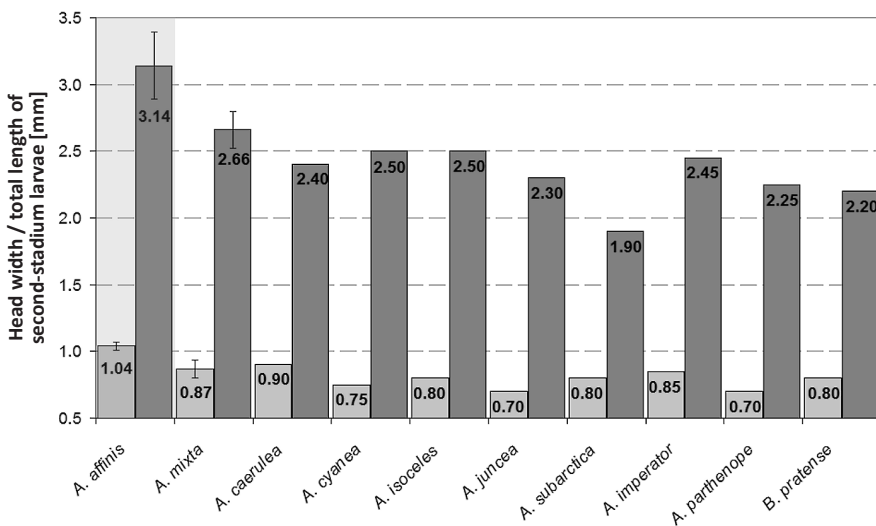

Figure 4. Head width/total length of second-stadium larvae in *Aeshna affinis* and *A. mixta* (with standard deviation). Values from data of this study, in other species from data out of literature (cf. Table 3). Bars in light grey represent head width, those in dark grey total length.

Considering head width of second-stadium larvae and exuviae, larvae of *A. affinis* had to grow less than those of *A. mixta*: Second-stadium larvae of *A. affinis* multiplied head width on average 7.0 times, those of *A. mixta* 8.3 times (Fig. 6). This difference was significant (U = 122.5, p < 0.0001).

In total, 172 larvae of *A. affinis* and 21 larvae of *A. mixta* were reared successfully from hatching to emergence. Complete larval development lasted between 62 and 110 days in *A. affinis* with a median of 95 days (Fig. 7). Females (n = 94, median = 94 d) developed faster than males (n = 78, median = 96 d), but the difference was not significant (U = 3 040.5, p = 0.054). Larval development in *A. mixta* took between 81 and 103 days with a median in both sexes of 91 days. In our rearing approach, larvae of *A. mixta* needed significantly less time to complete larval development than those of *A. affinis* (U = 2 423, p = 0.015) (Fig. 7) and had a significantly higher growth rate (U = 878.5, p < 0.0001) (Fig. 8).

To take temperatures during larval development into account, we expressed development in degree-day sums per larva. Median degree-day sums of
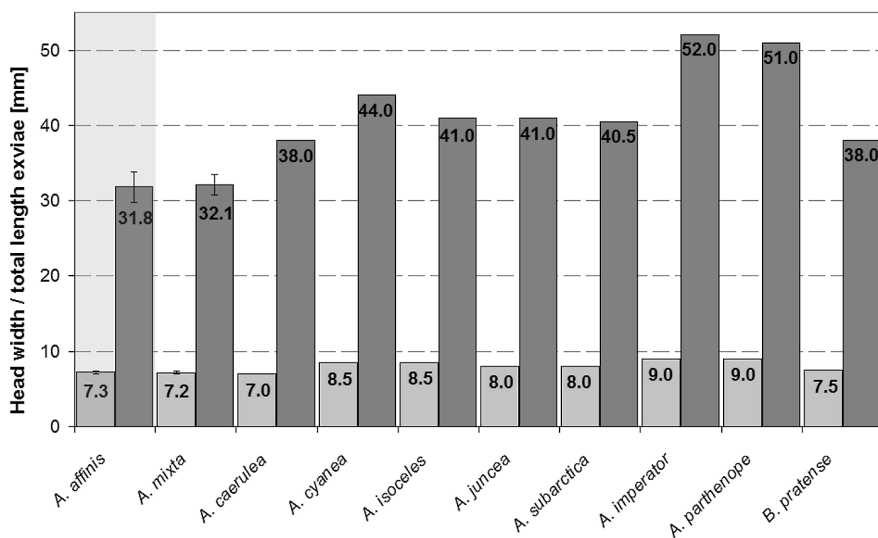

Figure 5. Head width/total length of exuviae in *Aeshna affinis* and *A. mixta* (with standard deviation). Values from data of this study, in other species average data were obtained by measuring each ten exuviae of the concerning species. Bars in light grey represent head width, those in dark grey total length.

A. affinis (1 298) and of *A. mixta* (1 469) differed significantly (U = 199, *p* < 0.0001) (Fig. 9).

Under rearing conditions, *A. affinis* emerged significantly earlier (U = 60.5, *p* < 0.0001) than *A. mixta*. Median emergence date of the first species was 20--vi-2009, of the latter species 08-vii-2009.

Larvae of *A. affinis* and *A. mixta* behaved completely differently. Those of *A. affinis* coexisted with conspecifics without any aggressive behaviour in their rearing containers. Only exceptionally hungry larvae preyed and fed on freshly moulted conspecifics. They never showed flight reactions when the containers were approached by persons. In contrast, larvae of *A. mixta* were very aggressive and attacked each other regularly. Cannibalism occurred even among equally sized larvae with sufficient food in their larval containers. When approaching the larval containers, *A. mixta* larvae usually showed flight reactions.
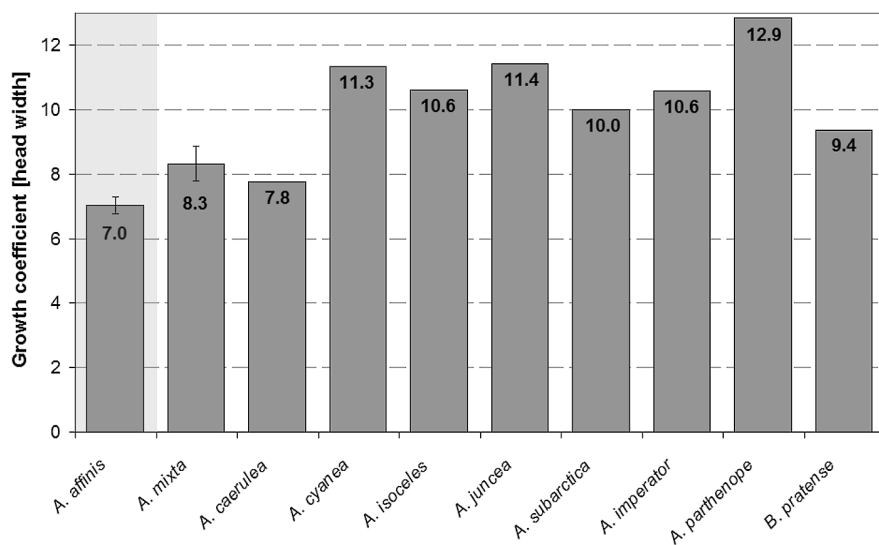

Figure 6. Growth coefficients of European Aeshnidae, calculated by dividing head width of exuviae by that of second-stadium larvae. Values of *A. affinis* and *A. mixta* from data of this study. In other species, growth coefficients were calculated by dividing average measurements of each ten exuviae by size data of second-stadium larvae from literature.
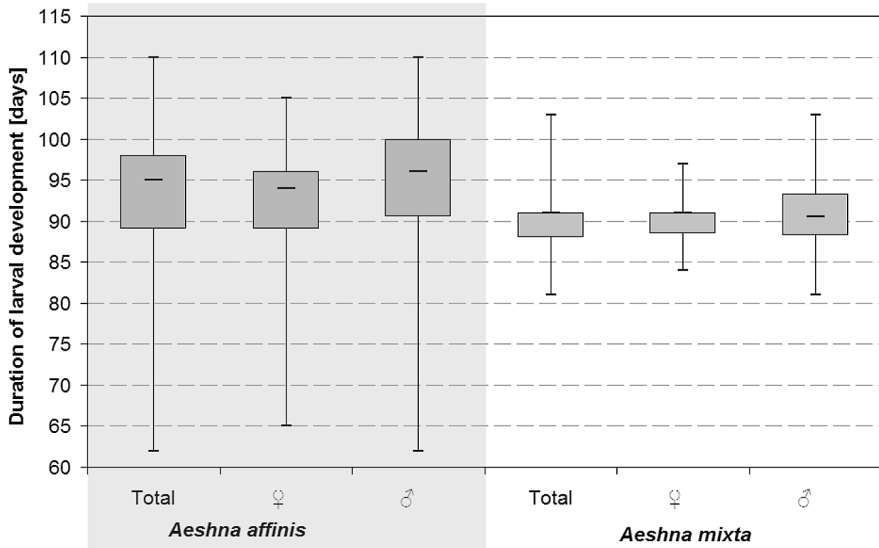
Figure 7. Duration of larval development in *Aeshna affinis* and *A. mixta*. Boxplots show maximum and minimum number of days, quartile 1, 3, and median number of days needed for development.
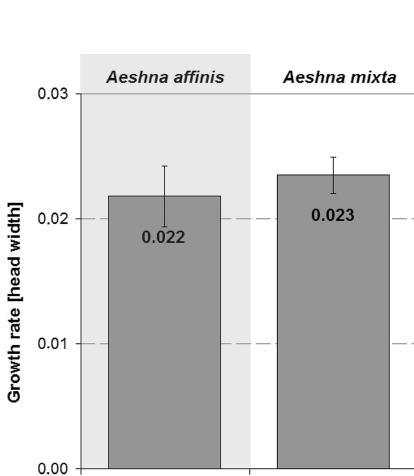

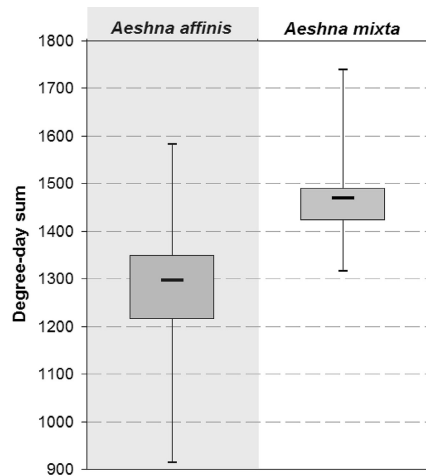**Figure 8.** Growth rates of *Aeshna affinis* and *A. mixta*.

Figure 9. Degree-day sums of *Aeshna affinis* and *A. mixta* in 2009.

Discussion

In our study, we aimed to find out whether there are developmental differences between larvae of *Aeshna affinis*, a species specialised in vernal pond conditions, and the less specialised congener *A. mixta* that reproduces mostly in permanent waters, but is also capable of developing in temporary ponds.

Vernal ponds are a distinctive type of temporary wetland typically filled by winter rains and/or melt water, drying out in the course of summer and for this reason usually being free of large predators such as fish or large dragonfly larvae (WELLBORN et al. 1996; 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 species, avoidance of predation and competition by other species apparently outweighs the great disadvantage of restricted water coverage. To cope with the risk of early drying-out of their larval habitats, specialised species are expected to be adapted by both early hatching and abridged larval development.

Aeshna affinis is the only European vernal pond specialist within the Aeshnidae. Hitherto, its life cycle and premature development are poorly known. Most authors (e.g., STERNBERG et al. 2000; KREKELS 2002; GRAND & BOUDOT 2006) suggest semivoltine development with drought resistant larvae. Referring to results of an emergence study carried out by BERNARD & SAMOLĄG (1997) in Poland, several authors (e.g., MONNERAT 2005; CORBET et al. 2006) assume univoltine development, but more detailed information is not available. Our data confirm the interpretation of an emergence study (BERNARD & SAMOLĄG 1997) according to which *A. affinis* displays univoltine development with overwintering in a diapause egg stage. The authors of the cited study suppose similar median hatching dates in *A. affinis* and *A. mixta*, but faster development in the former, which should enable it to complete larval development earlier in the course of the year. This hypothesis is now disproved by our results, because *A. mixta* developed faster than *A. affinis* (Fig. 8), although it had to moult one to two times more often than the latter (Table 3).

Table 3. Selection of exemplary studies about developmental features of European Aeshnidae, including data of this study. * – Hatching takes place after egg diapause, in the year after oviposition. ? – number of larval stadia unknown.

Species	Hatching date	Number of larval stadia	Larval development time	Source
Aeshna affinis	January to March*	9–10	62–110 days	BERNARD & SAMOLĄG (1997); SCHIEL & BUCHWALD (2015a)
Aeshna caerulea	June*	14–16	>3 years	STERNBERG (1990); STERNBERG & STERNBERG (2000)
Aeshna cyanea	March*	11–14 (16)	1–4 years	ROBERT (1959); SCHALLER (1960, 1977); DEGRANGE & SEASSAU (1964); NORLING (1984a); BEUTLER (1987); PETERS (1987); STERNBERG (2000); CORBET et al. (2006)
Aeshna grandis	May*	?	2–5 years	WESENBERG-LUND (1913); MÜNCHBERG (1930)
Aeshna isoceles	45–60 days after oviposition	?	1–2 years	GARDNER (1955); ROBERT (1959)
Aeshna juncea	(May) June/ July*	17–18	3–5 years	NORLING (1984a); STERNBERG (1990); STERNBERG (2000a)
Aeshna mixta	March to April (May)*	10–12	81–103 days, >1 year	MÜNCHBERG (1930); GARDNER (1950); SCHIEMENZ (1953); SCHALLER (1968, 1972); SCHALLER & MOUZE (1970); SCHIEL & BUCHWALD (2015a)
Aeshna subarctica	June/July*	16–18	3–4 years	STERNBERG (1990); STERNBERG (2000b)
Aeshna viridis	May*	13	1–3 years	MÜNCHBERG (1930); NORLING (1971); WITTENBERG et al. (2015)
Anax imperator	22–50 days after oviposition	13–16	few weeks – >1 year	PORTMANN (1921); CORBET (1954, 1957); ROBERT (1959); BEUTLER (1985); HOLMES & RANDOLPH (1994); CORBET et al. (2006); SCHIEL (2006)

Species	Hatching date	Number of larval stadia	Larval development time	Source
Anax ephippiger	10–12 days after oviposition	?	few weeks	HUNGER & SCHIEL (1999); STERNBERG (2000c); JÖDICKE (2003); CORBET et al. (2006)
Anax parthenope	3–9 weeks after oviposition	15	few weeks – >1 year	MÜNCHBERG (1932); ROBERT (1959); SCHIEMENZ (1953); SCHNAPAUFF et al. (2000); WERZINGER & WERZINGER (2001); CORBET et al. (2006)
Brachytron pratense	3–7 weeks after oviposition	15–16	1–2 years	MÜNCHBERG (1930); ROBERT (1959); HOLMES (1984)
Boyeria irene	April/May	?	2–3 years	FERRERAS-ROMERO (1997); WILDERMUTH (2005)

Concerning early hatching, our results support the hypothesis that the vernal pond specialist *A. affinis*, hatches earlier than the closely related permanent water species *A. mixta* (Fig. 1), and at significantly lower temperatures (BUCHWALD & SCHIEL 2015a). The strategy of early hatching after termination of egg diapause during the winter differs from other European representatives of the Aeshnidae (Table 3). Early hatching has already been demonstrated to be a strategy in temporary pond populations of *C. viridis* by DE BLOCK & STOKS (2004, 2005a) and DE BLOCK et al. (2005), and has also been shown in a comparative study of 15 European species (SCHIEL & BUCHWALD 2015a), including typical vernal pond species *Lestes barbarus* (Fabricius, 1798), *L. dryas* Kirby, 1890, and *Sympetrum flaveolum* (Linnaeus, 1758).

In addition to early hatching, fast larval development is an appropriate adaptation to avoid drought in immature water insects. Various studies (PADEFFKE & SUHLING 2003; JOHANSSON & SUHLING 2004; SUHLING et al. 2004) show that fast larval development is a reproductive strategy in temporary pond dragonflies under subtropical climatic conditions. Fast larval development is facilitated through physiological traits, such as high digestive efficiency (STOKS & MCPEEK 2003b), behavioural adaptations such as a high

activity level – fast life style – (Johansson & Suhling 2004), morphological aspects such as the absence of long abdominal spines for protection against fish predators (Wellborn et al. 1996), and a specific univoltine life history (Wellborn et al. 1996; Stoks & McPeek 2003a; Williams 2007). In our study, we focused on size and development time. Among other traits, fast development may be promoted by large size of larvae at hatching and a comparatively small size difference between second-stadium larvae and larvae of the final stadium. This reduces the number of larval stadia and the time needed to complete development.

Indeed, head widths of second-stadium larvae of *A. affinis* were significantly larger and size differences between second-stadium larvae and exuviae were significantly smaller than those of *A. mixta*. Furthermore, *A. affinis* needed fewer larval stadia than *A. mixta* and all other European Aeshnidae for which data is available.

According to an analysis of 85 Odonata species from 47 genera and 11 families, the number of larval stadia, including the prolarva, generally ranges from eight to 17 with a median of twelve stadia (Corbet 1999: 208). Therefore, the number of larval stadia in *A. affinis* is among the lowest of all Odonata species studied. This fits with the hypothesis of a low number of larval stadia in vernal pond specialists.

A comparison with the other European representatives of the family highlights the special developmental traits of *A. affinis*. The species has the largest second-stadium larvae (Fig. 4), one of the smallest final stadium larvae (Fig. 5), and the smallest growth coefficient (Fig. 6) of the European Aeshnidae for which data are available. Furthermore, the number of larval stadia is not only smaller than in *A. mixta*, but than in all other species (Table 3).

Growth rate and larval development time are influenced by environmental factors like photoperiod (e.g., Norling 1984b, 1984c; 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 the number of larval stadia and duration

of larval development under different climatic conditions in the different parts of the distributional ranges of the species considered in Table 3. In our study, only photoperiod and temperature changed. Larvae of *A. mixta*, which hatched later than those of *A. affinis*, experienced inherently longer photoperiods and higher water temperatures than *A. affinis* and the late-hatching *A. mixta* may have accelerated its growth rate and developed faster than *A. affinis* because water temperatures were higher later in the year. This explanation is supported by our analysis of degree-day sum (Fig. 9), which was significantly lower in *A. affinis* than in *A. mixta*.

Nevertheless, *A. affinis* completed larval development significantly earlier than *A. mixta* in our study because of its early hatching date.

Several studies carried out in temperate North America (e.g., Wissinger 1992; Wissinger & McGrady 1993), subtropical Africa (e.g., Padeffke & Suhling 2003; Johansson & Suhling 2004; Suhling et al. 2004, 2005), and tropical Central America (e.g., Fincke 1992, 1994) suggest intraguild predation is an important factor influencing the composition of larval communities in small and/or temporary water bodies. These studies show that even »subtle differences in phenology and/or size-specific shifts in habitat distribution can lead to the potential for asymmetric interspecific interactions« (Wissinger 1992). Concerning the life history of *A. affinis,* the early hatching date and large second stadium larvae may promote the species' development by a priority effect, which allows it to suppress less specialised congeners by intraguild predation. On the other hand, if a temporary pond does not dry out, species composition will shift and the specialised species may be outcompeted by larvae of permanent pond species that are already present in the pond having over-wintered from the previous year when the specialists hatch in the spring after oviposition.

As hypothesised here, and already demonstrated in vernal pond species of the zygopteran genus *Lestes* (Schiel & Buchwald 2015b), the following developmental traits are put into effect in *A. affinis*: i) early hatching date; ii) large second-stadium larvae that have to grow less and with fewer larval stadia than those of permanent water species; iii) short larval development time, although longer than that of *A. mixta*; and iv) significantly lower degree-day sums than in their less specialised counterparts.

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