

# Bivoltinism in *Coenagrion mercuriale* (Zygoptera: Odonata) in the southern margin of its distribution range: emergence pattern and larval growth

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Voltinism is an important life history trait that varies with the environment. In temperate zones, insect populations take a substantially longer time to reach the adult stage in the northern compared to the southern regions. In this study, emergence pattern and larval growth of the threatened zygopteran (Odonata) *Coenagrion mercuriale* were investigated in a population located in the southern limit of its distribution range in order to determine its life history strategies in a hot climate and compare them to those displayed in northern populations. There was no apparent winter diapause. The species produced two generations in a year, with the first generation emerging in mid spring and the second in late summer. The emergence pattern of the first generation was typical of a summer species and lasted 48 days. All larvae emerged by the end of May. Due to some environmental perturbations, the emergence pattern of the second generation was not surveyed, but there was evidence that the emergence season was short (21 days). Larval structure prior to the second emergence of the year showed that only 25 % of the population was in the final instar, which explains the shorter emergence season. We assume that the first eggs laid in the spring hatch and grow rapidly to reach the final instar in late summer as a consequence of higher temperatures and potential high food availability. There was a significant seasonal decline in body size in both males and females. The second generation had a significantly smaller body size, presumably due to the short growth season and/or higher growth rate.

**Key words:** voltinism, Odonata, endangered, emergence.

## INTRODUCTION

In temperate zones, the number of generations per year (voltinism) in insects is often plastic and thus depends on the local environment (Iwasa *et al.* 1994; Corbet *et al.* 2006; Altermatt 2009; Chen *et al.* 2011). Patterns of voltinism (semi-, uni-, bivoltine) have been well documented in odonates (dragonflies and damselflies), showing an increase in generation time with increasing latitude (Corbet *et al.* 2006; Flenner *et al.* 2010). Temperature and photoperiod are the main environmental factors that vary over a latitudinal gradient; higher temperature and longer days induce higher growth and thus reduce the time required to complete a generation (Norling 1984; Corbet 1999). Therefore, a species whose distribution covers a

large latitudinal range in a temperate zone is likely to express marked plasticity in voltinism; for instance, *Enallagma cyathigerum* is a semivoltine at 56°N (Parr 1976; Corbet & Chowdhury 2002), univoltine at 47–53°N (Steinmann 1961; Steiner *et al.* 2000), and bivoltine at 48–52°N (Smock 1988; Burbach 2000). Another important factor that impacts growth rate is habitat (Corbet *et al.* 2006). Odonate species that live in temporary waters usually have rapid growth rates and are able to complete at least one generation per year (Suhling *et al.* 2005). Species that inhabit perennial waters, on the other hand, typically have slower growth and often need more than one year to produce a generation (Suhling 2001). However, not much information is available on seasonal regulation of

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odonates that are specific to shallow and slow-flowing streams where water temperature is highly dependent on the local environment.

*Coenagrion mercuriale* is an Atlanto-Mediterranean damselfly that lives in ditches, springs and brooks (Boudot 2006). Even though its distribution expands as far north as the U.K., the main global population is centred in southern Europe where it is listed as endangered in the IUCN red list of most countries due to severe population declines a result to loss of habitat (Boudot 2006). *C. mercuriale* has been well-studied in the U.K. (Purse & Thompson 2002, 2003; Purse *et al.* 2003; Rouquette & Thompson 2004; Watts *et al.* 2005, 2007; Watts & Thompson 2012) where the species completes a single generation in two years (*i.e.* it is semivoltine) (Corbet 1957; Purse & Thompson 2003). Because most second-year larvae overwinter as antepenultimate, penultimate and final instars, the species displays a summer species pattern of emergence (Purse & Thompson 2002, 2003). One observation of univoltinism (one generation per year) was recorded in Germany in a stream affected by industrial water-cooling which increased the local water temperature (Thielen 1992). Moreover, a lack of genetic differences between different voltinism cohorts of *C. mercuriale* implies that some larvae can either accelerate or delay their development (Watts *et al.* 2005; Watts & Thompson 2012). These findings suggest that voltinism in *C. mercuriale* is plastic, and likely varies with the environment (*e.g.* latitude). This raises some key questions regarding its life history pattern (including larval population structure, temporal pattern of emergence, and the number of generations per year) in the southern limits of this species' distribution where it has not been well-studied.

The present study investigates seasonal regulation and temporal pattern of emergence of *C. mercuriale* in a population located at the southern limit of its geographic range (North Africa), a region where annual temperatures are substantially higher than the rest of the species' distribution range.

## MATERIAL AND METHODS

### Study site

The study was conducted in the Old Bridge Canal (OBC) which is a shallow artificial stream of about 450 m that flows into the Seybouse River upstream, Guelma, Algeria (36°28'N 7°22'E) (Khelifa *et al.* 2011). Annual water temperature

was 13.9 °C, pH was 8, and dissolved oxygen was 11.37 mg/l. The downstream part of the OBC, where the *C. mercuriale* population occurs, is dominated by *Typha angustifolia*. Large populations of *Orthetrum nitidinerve*, *O. chrysostigma*, and *O. coerulescens* also inhabit this part of the stream (Khelifa *et al.* 2013).

### Emergence pattern

Using previous knowledge on the species' flight period (Khelifa *et al.* 2011), daily field visits started in late March 2013 to record the onset of the emergence season. In order to reduce the trampling effect on larvae at the study site, we placed some stones in areas where emergent supports were difficult to access in order to create a path that facilitates collection of exuviae. Every day, we surveyed a 50-m transect for exuviae in the late afternoon (16:00). We are confident that no exuvia were left after each sampling and we considered that emergence had stopped when no exuvia were recorded for seven consecutive days. Since the study population is located in the southern limit of the temperate zone where bivoltinism was recorded in some odonates (Corbet *et al.* 2006), we expected that the species could have a second generation. Therefore, after the end of the first emergence period surveys were conducted every week. Sampling then switched to a daily basis when the second emergence started (in late summer), and encompassed the same study area as in the first emergence season. Exuvia body length (from the top of the head to the tip of caudal lamellae), head width, and posterior wing sheath length were measured to the nearest mm with a digital calliper. EM50, the number of days after which half of the population emerges, was calculated for both sexes. Sex ratio at emergence was estimated using exuviae.

### Larvae growth and population structure

From December 2012 to August 2013 (except July), monthly larvae collections were carried out using a rectangular hand net of 0.5-mm mesh in three different sampling points (20 m apart) in the last week of the month. In the laboratory, body length (with and without caudal lamellae) and head width were measured with a digital calliper to the nearest mm (small larvae were measured under a dissecting microscope). After measurements, larvae were kept in aquaria (five larvae per aquarium to avoid cannibalism) and returned to

their original location within 24 h. Larvae were grouped into four different instar groups (C–F) (Purse & Thompson 2002) using the criteria described by Corbet (1955). Groups F, E, D represent final instar, penultimate, and antepenultimate, respectively, while group C corresponds to instars 9 to 10.

**Statistical analyses**

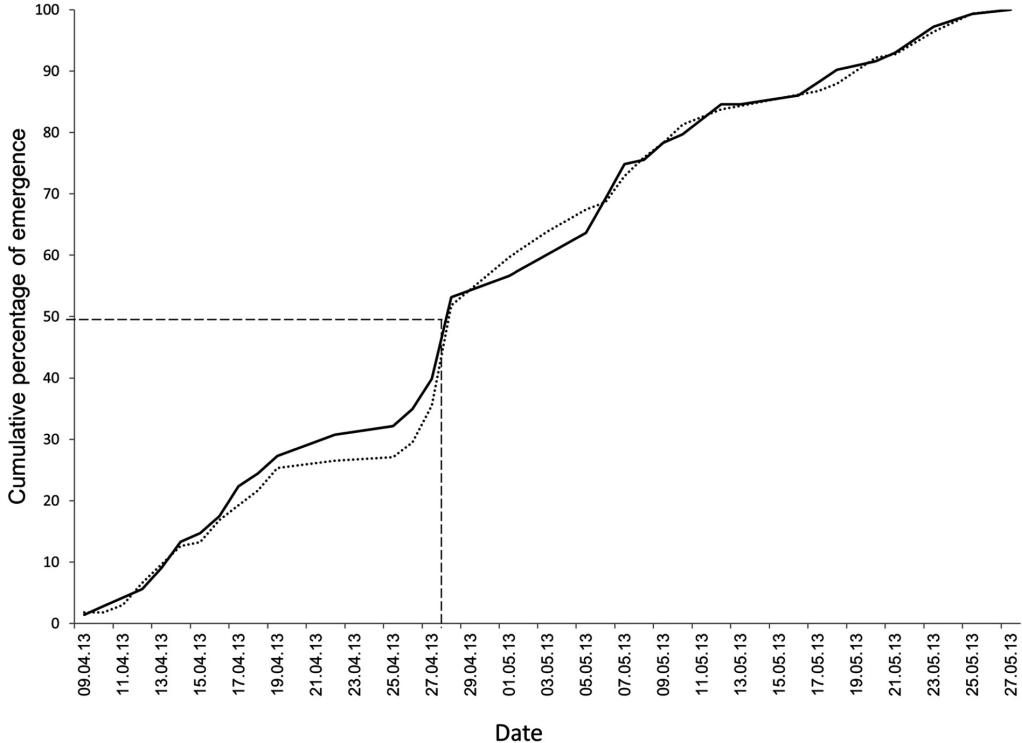
All statistical analyses were completed with R 3.0.1 (R Core Team 2014). We tested the residuals of the response variables for normality and homogeneous of variance. A chi-square test was conducted to see whether sex ratio at emergence deviated from 1:1. A Kolmogorov-Smirnov two-sample test was used to identify any difference in the emergence curve between sexes. Two-sample chi-square tests were carried out to assess for significant differences in the proportion of larvae across instar groups between months. Welch two-sample *t*-tests were used to compare morphological traits of final instar exuviae between generations. Wilcoxon tests were carried out to look for differences in morphological traits between

sexes. We carried out ANCOVA to test whether there is a seasonal decline in size and test for potential significant difference in the slope of sexes in both body length and posterior wing sheath length; the latter analysis was not carried out on head width because it was not normally distributed even after attempts at transformation. All morphometric values presented are mean ± S.D.

**RESULTS**

**Temporal pattern of emergence**

Stream water had a maximum temperature of 17.7 °C in early May and 19.3 °C in late August. A total of 317 final instar exuviae were collected between 9 April and 27 May, 2013. The total emergence season of the first cohort lasted 48 days with a peak in late April. Sex ratio was slightly male biased (53.3 %) but it did not significantly differ from unity ( $\chi^2 = 1.39$ , d.f. = 1,  $P = 0.23$ ). EM50 was 23 days for both males and females (Fig. 1) and their temporal pattern of emergence was similar (Kolmogorov-Smirnov two-sample test:  $D = 0.11$ ,  $P = 0.97$ ). There was a significant seasonal decline



**Fig. 1.** Emergence curve of the first generation of a bivoltine *Coenagrion mercuriale* population. Continuous and dotted lines indicate females and males, respectively. Vertical dashed line represents EM50.

**Table 1.** Summary of the ANCOVA for body length and posterior wing sheath length pattern during the emergence season in the first generation of *Coenagrion mercuriale*.

		Estimate	S.E.	t-value	P-value
Body length	Intercept	17.344	0.181	95.416	0.0001
	Sex [M]	-0.790	0.247	-3.197	0.001
	Season	-0.025	0.007	-3.460	0.0006
	Sex [M]:Season	-0.001	0.009	-0.181	0.856
Posterior wing sheath length	Intercept	4.190	0.044	94.037	0.0001
	Sex [M]	-0.191	0.063	-2.996	0.002
	Season	-0.004	0.001	-2.528	0.012
	Sex [M]:Season	-0.001	0.002	-0.473	0.630

Multiple  $R^2 = 0.25$ , d.f. = 234,  $F = 26.14$ ,  $P < 0.0001$ ; 'M' = male.

in body length (Table 1, Fig. 2a) and posterior wing sheath length (Table 1, Fig. 2b) in both sexes. The decreasing rate was not significantly different between sexes but females were significantly larger than males throughout the entire emergence season (Table 1).

A second generation started to emerge on 19 August and exuviae continued to be found until 27 August. On 28 August, the environment around the stream was degraded due to flooding, after which no exuviae could be recorded even though teneral (immature individuals) continued to be observed up to 6 September. Sixty-three exuviae were collected over this 8-day period, but given the presence of teneral the second emergence season lasted some 18 days.

There were significant differences in body length, head width, and posterior wing sheath length between seasons in both sexes (Table 2). However, marked sexual size dimorphism was apparent in the first generation (Wilcoxon test:  $W = 8226.5$ ,  $P < 0.0001$ ;  $W = 3965$ ,  $P < 0.0001$ ;  $W = 5202$ ,  $P < 0.0001$  in body length, head width, and posterior wing sheath length, respectively), and not in the second one (Wilcoxon test:  $W = 271.5$ ,  $P = 0.94$ ;  $W = 227$ ,  $P = 0.60$ ;  $W = 201$ ,  $P = 0.47$  in body length, head width, and posterior wing sheath length, respectively).

### Larval population structure

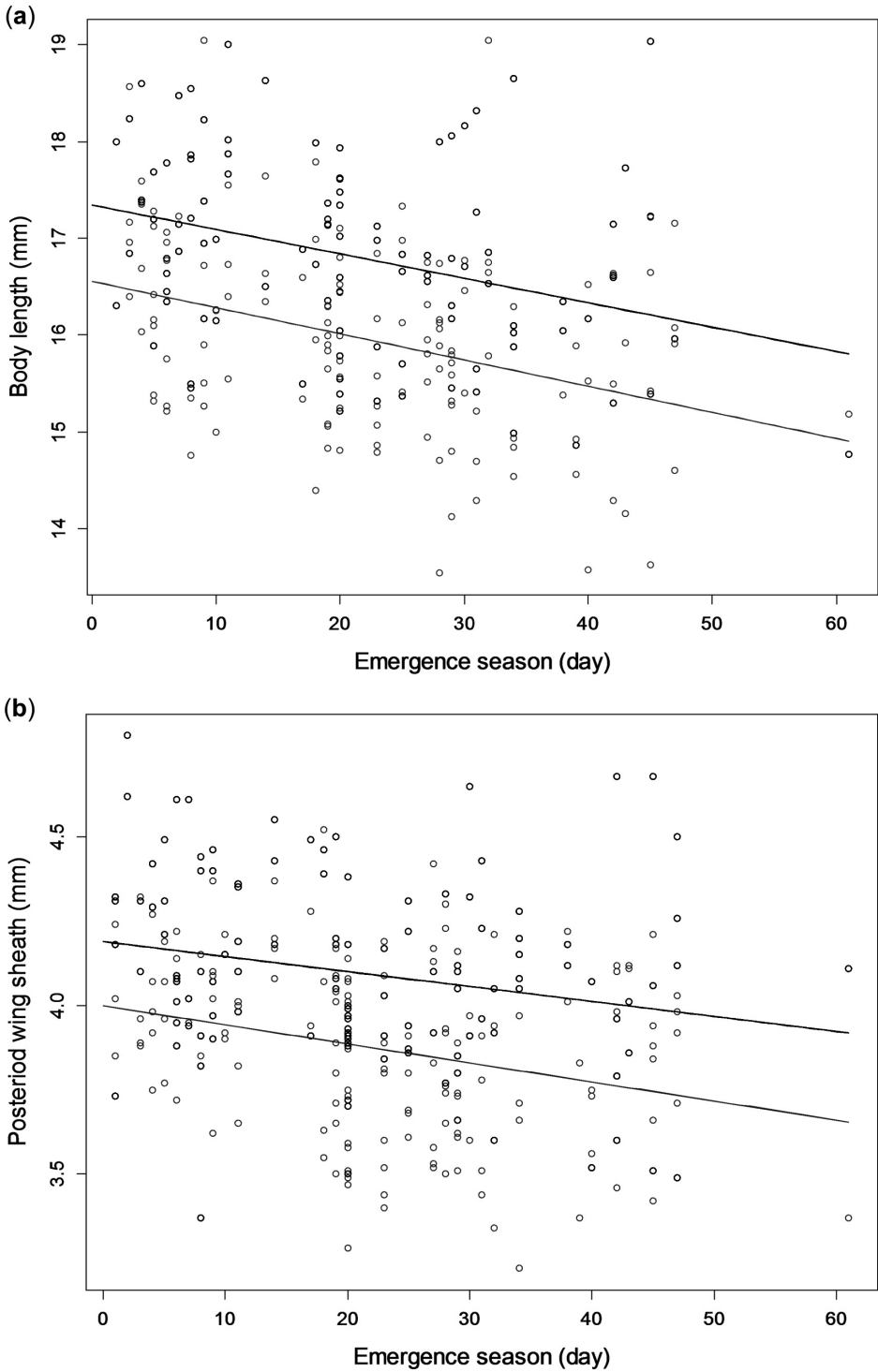
A total of 103 larvae were collected during the study period but no larva was found during May and June. Table 3 presents morphological measurements of the four final instar groups, and it shows a substantial variability in size within each group. There was no significant difference in the frequency distribution of instars from month

to month between December and April (Table 4). Between December and March, there was no indication of diapause in larvae that had not reached the final instar (Fig. 3). In early winter (December), about 80 % of larvae sampled were equally distributed among penultimate and final instar while the remaining 20 % were equally distributed between groups C and D. Group C was not recorded after December and group D was not observed after January (Fig. 3). In March prior to the first emergence of the year, 94.1 % of larvae were in the final instar while only 5.9 % were penultimate. In August, prior to the second emergence of the year, final instar larvae represented 25 %, antepenultimate represented 6.3 %, and the remaining proportion was evenly distributed between groups C and D (37.5 % and 31.2 %, respectively).

### DISCUSSION

According to the literature, voltinism of *C. mercuriale* is likely to be dependent on latitude. The present study provides a piece of the puzzle that has been missing about the seasonal regulation of *C. mercuriale* at its southern distribution range. We provide the first evidence that *C. mercuriale* is bivoltine at the southern edge of its range, using a combination of monitoring the temporal pattern of emergence through exuviae and by characterizing the larvae population structure.

Although *C. mercuriale* has a moderately long flight season (lasting until autumn) in some southern populations (Dijkstra & Liwington 2007), the question of whether this developmental pattern is due to protracted larval emergence or a bivoltine life history was not known until now. In the U.K. and central Europe, the species is



**Fig. 2.** Seasonal pattern in body size of *Coenagrion mercuriale* exuviae during the first generation; **a**, body length; **b**, posterior wing sheath length. Black and grey symbols indicate females and males, respectively.

**Table 2.** Body length, head width and posterior wing sheath length of final instar exuviae in two subsequent generations of a bivoltine population of *Coenagrion mercuriale*.

Sex	Traits	Generation 1	Generation 2	P-value
Female	Body length (mm)	16.81 ± 1.00	14.37 ± 0.89	0.0001
	Head width (mm)	3.26 ± 0.29	2.84 ± 0.45	0.0002
	Posterior wing sheath (mm)	4.09 ± 0.27	3.77 ± 0.28	0.0001
Male	Body length (mm)	15.95 ± 1.00	14.38 ± 1.06	0.0001
	Head width (mm)	3.10 ± 0.31	2.76 ± 0.35	0.0001
	Posterior wing sheath (mm)	3.87 ± 0.27	3.73 ± 0.24	0.01

P = level of significance of Welch two-sample t-test.

**Table 3.** Mean head width and body length, with and without caudal lamellae, for four distinct instar groups of larval *Coenagrion mercuriale*.

Group	Head width (mm)	Body length with CL (mm)	Body length without CL (mm)
C	1.80 ± 0.15	11.39 ± 1.82	8.49 ± 1.20
D	2.43 ± 0.14	12.37 ± 2.92	9.70 ± 1.44
E	2.95 ± 0.16	15.06 ± 1.93	11.52 ± 1.86
F	3.54 ± 0.22	17.42 ± 2.01	13.58 ± 2.01

CL = caudal lamellae. C–F are larval instar groups.

semivoltine (Corbet 1957; Sternberg 1999; Purse & Thompson 2002), though there is genetic evidence that, at least some, larvae are capable to alter their developmental period (Watts *et al.* 2005; Watts & Thompson 2012). In Germany, Thielen (1992) recorded a univoltine population of *C. mercuriale*, most likely due to a local increase in water temperature resulting from industrial activities. This is not surprising since many field and experimental studies have shown that temperature affects growth rate and thus determines voltinism (Corbet 1999; Flenner *et al.* 2010). In North Africa, water temperature is higher than central and even southern Europe. Also, it is possible that high food availability as observed at the study site (high densities of amphipods) provides optimal conditions in which eggs that are laid in early spring were able to hatch, develop rapidly and emerge in late summer.

Emergence season of the first generation of *C. mercuriale* began in early April, which is a month earlier than in northern populations (Corbet 1962; Purse & Thompson 2003). This difference might be the result of a higher growth rate in our study population (low latitude) compared to northern populations (high latitude), as it was shown in a

**Table 4.** Chi-square tests comparing the distribution of larvae of *Coenagrion mercuriale* across groups (C–F) and between months.

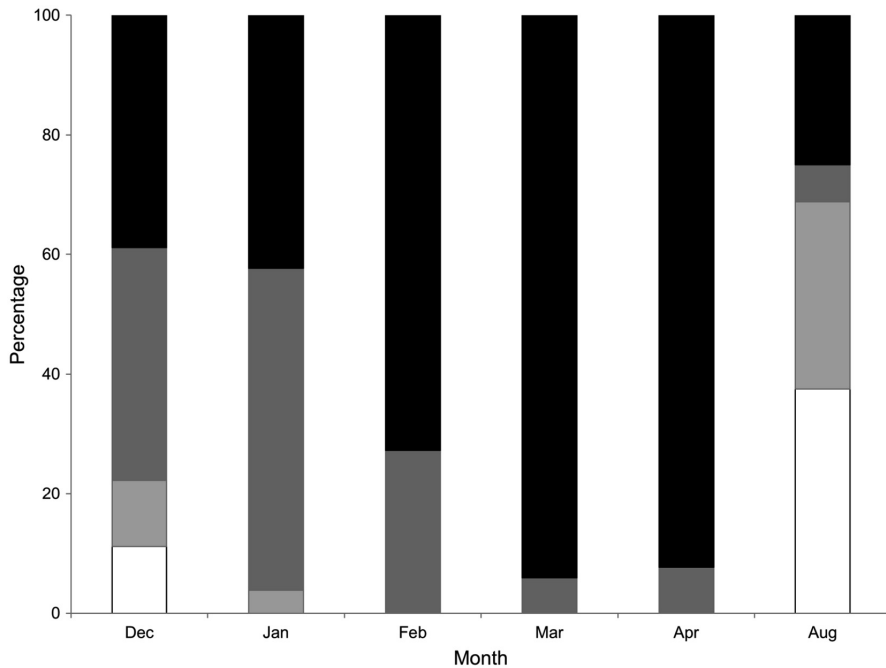
	$\chi^2$	d.f.	P
Dec vs Jan	4.24	3	0.23
Jan vs Feb	8	6	0.23
Feb vs Mar	8	4	0.09
Mar vs Apr	8	4	0.09
Apr vs Aug	14.84	3	0.001
Aug vs Dec	8.51	3	0.03

Dec, Jan, Feb, Mar, Apr, Aug are abbreviations of months.

congeneric species (*C. johanssoni*) (Šniegula *et al.* 2012). The study population displayed a summer species life history pattern due to the fact that emergence was asynchronous showing an EM50 (23 days) comparable to that presented in British populations (25 days) (Corbet 1962; Purse & Thompson 2003). However, the emergence season recorded in our study was substantially shorter with 48 days compared to 66 days (Purse & Thompson 2003). Furthermore, in contrast to our study in which sex ratio at emergence was roughly unity, implying both sexes experience comparable mortality at egg and larval stages, whereas Purse & Thompson (2003) recorded a significant male bias. In addition, similarly to our study, temporal pattern of emergence (*i.e.* the curve shape) of *C. mercuriale* in the U.K. did not differ between sexes, which is typical in zygopterans (Corbet & Hoess 1998). The seasonal decline in body size, which again is typical in zygopterans (*e.g.* Purse & Thompson 2003; Lowe *et al.* 2009), was similar in both sexes, albeit with Purse & Thompson (2003) finding that female body size decreases more rapidly than does male body size.

The second generation started to emerge in late August when temperatures were 1.6 °C higher





**Fig. 3.** Percentage of *Coenagrion mercuriale* larvae of the four last instar groups during the wintering season and prior to emergence. White and light grey, dark grey and black shading represent groups C, D, E, F, respectively. No larvae were found in May and June.

than those encountered in the spring. Unfortunately, we were not able to survey the entire emergence season because of a flood that probably shifted much of the *C. mercuriale* larval population downstream. Based on observations on teneral, however, we estimated an emergence period of 18 days, which was consistent with the larval population structure recorded in late summer when only a small proportion of larvae were at the final instar. One interesting finding is the smaller body size of the late-emerging exuviae compared with the ones collected in the spring. This could be explained by a combination of the shorter developmental period *per se* and some aspect of either Bergmann's rule or the temperature-size rule (Blanckenhorn & Thorn 2004; but see Shelomi 2012), whereby many ectotherms grow faster but have a smaller body size in warmer environments (see Hassall *et al.* 2014 for example in odonates). We assume that larvae grew rapidly through the summer due to the high temperature, but this occurs at the expense of smaller size. Since fitness is associated with body size in many insects, including odonates (Sokolovska *et al.* 2000), this could have significant implications on individual reproductive success (Corbet 1999; Khelifa *et al.* 2012);

however, an extensive study of fitness components in the congener *Coenagrion puella* found little impact of body size upon fitness (Thompson *et al.* 2011).

According to our observations, it could be assumed that *C. mercuriale* undertakes a direct post-embryonic development: larvae did not show any sign of winter diapause unlike other European populations (Corbet 1962; Thielen 1992; Sternberg 1999; Purse & Thompson 2002). One explanation for this difference is that the minimum temperature threshold for development that triggers larval diapause in European odonates (Thompson 1978; Duffy 1994; Corbet 1999) was not reached during the winter in our study stream in which larval population structure was characterized by an increased synchrony throughout the wintering season. Purse & Thompson (2002) recorded similar population structure of the second-year larvae prior to winter in the U.K., *i.e.* most larvae reached the three last instar groups (D, E and F). However, prior to emergence larvae in our study were more synchronous than the overwintering British population in which the proportion of penultimate larvae was larger than those at the final instar (Purse & Thompson 2002). The result of larval

diapause was a more asynchronous emergence in the British population compared to the study population. The fact that no larva was collected in late May and late June confirms that the entire population (first generation) emerged in late spring. Given that the reproductive season of *C. mercuriale* lasts about two months (Mahdjoub *et al.* 2014), we assume that the first eggs laid by the first generation would hatch and grow with a high rate in order to reach final instar in late August. Larval population structure in late summer indicated that only a fraction of the population emerges and forms the second generation of the year (partial bivoltinism). The remaining smaller larvae would continue their development and emerge in the spring of the next year. Similar life history patterns were recorded in other Coenagrionidae like *Erythromma lindenii* in the southern Iberian Peninsula (Ferrerias-Romero 1991; Ferrerias-Romero & García Rojas 1995) and *Enallagma aspersum* in North Carolina (Ingram & Jenner 1976). The con-

sequence of a partial bivoltinism is usually a high variability in size at emergence during the spring, as was observed in the present study.

We showed that *C. mercuriale* is bivoltine in the southern limits of its distribution range which highlights the plasticity of its voltinism along its geographic range. This finding helps to predict the effects of climate warming on the future life history dynamics of the species along the latitudinal gradient. We expect that some southern European populations can have a partial bivoltinism, similar to the one described in the current study. Future research should focus on the effects of the changes in life history on community interactions and the population dynamics of this threatened damselfly.

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