

Water temperature drives local variability in the life cycle of *Onychogomphus forcipatus* (Odonata: Gomphidae) in a Mediterranean river

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ABSTRACT

Water temperature drives local variability in the life cycle of *Onychogomphus forcipatus* (Odonata: Gomphidae) in a Mediterranean river.

Geographic variation in life history traits of dragonflies has been extensively studied, mainly along latitudinal clines, but life history variation at a local scale has received less attention. We describe the life cycle differences between two populations of *Onychogomphus forcipatus unguiculatus* (Odonata: Gomphidae) located in close proximity in a small Mediterranean river basin in the northeast of the Iberian Peninsula. While the larval growth pattern recorded in the middle course of the river showed an exclusively univoltine pattern, the one found in one of its tributaries revealed a mixed pattern of uni- and semivoltinism. The difference in water temperature between these sites, especially during the cold months, is probably the environmental factor underlying the differences in voltinism. Given the spatial proximity between the two populations, 7.5 km apart on a straight line, our finding suggests phenotypic plasticity of this taxon as the mechanism of adjustment of its life cycle to small variations in water temperature. Overall, our results may help to understand how this species can respond to variations in water temperature under climate change or other human-mediated impacts.

KEY WORDS: Larval development, lower thermal threshold, accumulated degree days, diapause, seasonal regulation, voltinism, phenotypic plasticity.

RESUMEN

La temperatura del agua determina la variabilidad local del ciclo de vida de *Onychogomphus forcipatus* (Odonata: Gomphidae) en un río mediterráneo.

La variación geográfica del ciclo de vida de los odonatos ha sido estudiada principalmente a lo largo de clinas latitudinales pero su variabilidad a escala local ha recibido mucha menos atención. En este artículo describimos las diferencias en el ciclo de vida de dos poblaciones muy próximas de *Onychogomphus forcipatus unguiculatus* (Odonata: Gomphidae) en la cuenca de un pequeño río mediterráneo en el noreste de la península Ibérica. Mientras que el patrón de crecimiento larvario registrado en el curso medio del río se correspondió con el de un ciclo de vida exclusivamente univoltino, el observado

en un arroyo afluente coincidió con uno mixto uni- y semivoltino. La diferencia en la temperatura del agua entre ambas localidades, especialmente durante los meses fríos, es probablemente el factor ambiental causal de las diferencias en el voltinismo. Dada la proximidad geográfica entre las dos poblaciones, separadas 7.5 km en línea recta, nuestro hallazgo sugiere la plasticidad fenotípica de este taxón como el mecanismo de ajuste de su ciclo de vida a pequeñas variaciones en la temperatura del agua. En general, nuestros resultados pueden ayudar a entender cómo esta especie puede responder a variaciones de la temperatura del agua provocadas por el cambio climático u otros impactos de origen humano.

PALABRAS CLAVE: Desarrollo larvario, umbral térmico inferior, grados día acumulados, diapausa, regulación estacional, voltinismo, plasticidad fenotípica.

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INTRODUCTION

Organisms adapt to environmental conditions by adjusting their life history traits. The geographic variation in the life cycle duration of insects is associated with the length of the growing season and so is related to variables like temperature and photoperiod (Wolda, 1988; Lankinen *et al.*, 2023). In temperate zones, the cold season is an obstacle for the continuous growth of insects, all the more so at higher latitudes. To cope with unfavorable conditions and to control the timing of sensitive stages insects commonly undergo dormancy in the form of diapause, a hormonally controlled state of physiological rest (Denlinger, 2022). As a result of a shortened growing season at higher latitudes and altitudes, life cycles tend to lengthen, leading to patterns of one generation or less per year (Zeuss *et al.*, 2016; Kong *et al.*, 2019).

In dragonflies, the aquatic larval stage is usually the best adapted to survive the cold season. Hence, in order to avoid unfavourable conditions for survival and reproduction, the emergence of the terrestrial adult is prevented by means of regulatory mechanisms well before the arrival of winter. These mechanisms also determine the appropriate times for resuming development when suitable conditions are reestablished (Corbet, 1999).

Norling (1984, 2021) discussed the main lines of seasonal regulation in odonates of the temperate zone. The long photoperiods typical of summer induce an initially weak diapause-like state—an ultimately winter-preparing or regulatory process—slowing down the development of the larvae in late stadia, in general more strongly in the antepenultimate (F-2) and penultimate (F-1)

ones. This prevents untimely emergence and can, in some late-emerging populations, even counteract overwintering in the last stadium (F-0). Subsequently, often after some further moulting during intermediate photoperiods, shorter end-of-growing-season photoperiods induce a winter diapause that halts development and improves winter survival. Winter growth, though, can occur in warmer climates, in a mild diapause state, if not leading to premature emergence. Depending on the size that larvae had reached before the previous winter, higher temperatures and the progressively longer photoperiods during the following spring stimulate larval growth or delay it. Larvae that reached or exceeded a winter critical size (WCS) will develop rapidly and emerge, while those smaller than the WCS will soon enter the slow growth of the long-day diapause and remain in the water for one more winter. The WCS is in part genetically determined at a species and population level but is also modified by environmental factors such as the combination of temperature and photoperiod in spring.

The assessment of voltinism, i.e., the number of generations completed within one year, is useful for understanding how life cycles adapt to environmental conditions, especially regarding latitude. There is a considerable number of studies showing that the voltinism of dragonflies varies latitudinally following the cline of temperature and photoperiod (reviewed by Corbet *et al.*, 2006). At a local scale, fluctuations in physicochemical and biological conditions (prey availability, competition, predation...) may play a role in modulating the latitudinal patterns (Baker & Clifford, 1981; Suhling, 1995). Field studies at a local level provide insights to identify the causes of life history and voltinism variation across

populations and species (Braune et al., 2008; Samraoui et al. 2023) and are the first step in assessing their vulnerability to climate change (Ott, 2010; Hassall & Thompson, 2008).

Onychogomphus forcipatus (Linnaeus, 1758) is a latitudinally widespread western Palaearctic species that can be found from North Africa, the Aegean islands, the Levant, and Turkmenistan to the Scandinavian peninsula and European Russia. Based on Boudot et al. (1990), it can be divided into three subspecies, *O. f. forcipatus* (Linnaeus, 1758), *O. f. unguiculatus* (Vander Linden, 1823) and *O. f. albotibialis* Schmidt, 1954, with distribution ranges that do not overlap except in some small areas, e.g., in South East France and Northern Spain (Mezquita-Aranburu & Torralba-Burrial, 2015), where the first two live in sympatry. It is the most common and widespread gomphid in Europe (Boudot & Kalkman, 2015; Schneider & Dumont, 2015).

The ssp. *unguiculatus* (Vander Linden, 1820) is found in the Iberian Peninsula, South East France, Italy and the Maghreb (Morocco, Algeria and Tunisia) where it inhabits sunny or partially shaded slow to moderately fast-flowing rivers and streams. The channel substrate is usually a mixture of sand, gravel and cobbles. It is general-

ly found in the lowland and up to mid-mountain in southern Europe (1200 m a.s.l.) and the Maghreb (1600 m a.s.l.) (Boudot & Kalkman, 2015).

Onychogomphus forcipatus shows variability in the duration of its life cycle. It has been described as completing it in three to five years (Dreyer, 1986), three to four years (Schiemenz, 1953) and three years (Herden, 1990) in Germany; three to four, even up to five, in Switzerland (Robert, 1959); two to three in Upper Austria (Chovanec, 2019) and the south of France (Suhling, 2001) and two years in southern Spain (Ferrerías-Romero & García-Rojas, 1995) and in Algeria (Samraoui et al., 2024).

In Martín & Maynou (2023) we described a univoltine population of *O. forcipatus unguiculatus* from the small Mediterranean Tordera River in northeastern Spain. This finding was unexpected given that the records from the Iberian Peninsula and northern Africa pointed to a life cycle of at least two years and it begged the question of whether univoltinism was also the pattern in other watercourses of the Tordera basin or if there was intraspecific variation.

In this article, we aim to explore the voltinism patterns of two different populations of *O. forcipatus unguiculatus* located in close proximity

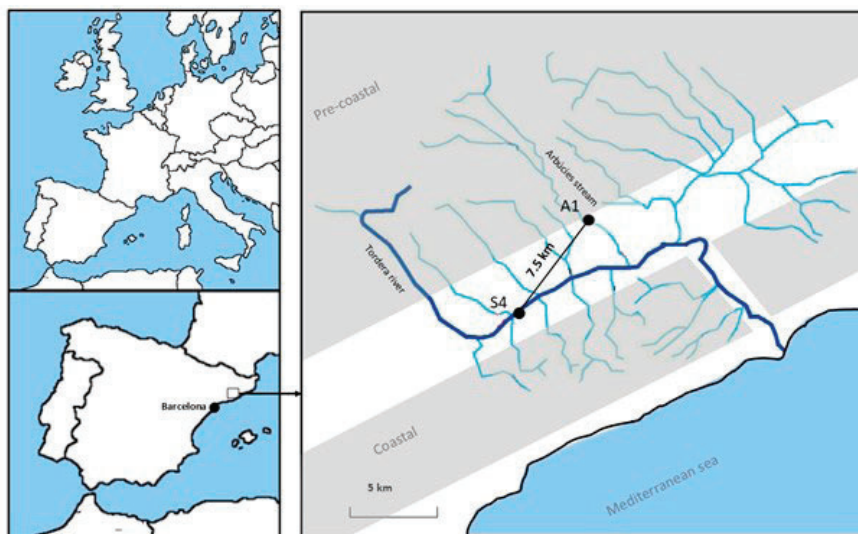


Figure 1. Location of the Tordera River basin and the sampling sites S4 (Tordera River) and A1 (Arbúcies stream) (solid circles). The Arbúcies stream flows into the middle course of the river. Shaded areas in the panel on the right represent the Coastal and Pre-coastal mountain ranges. Maps obtained from the Catalan Water Agency. *Ubicación de la cuenca del río Tordera y de los puntos de muestreo S4 (río Tordera) y A1 (riera de Arbúcies) (círculos sólidos). La riera de Arbúcies desemboca en el curso medio del río. Las zonas sombreadas del panel de la derecha representan las cordilleras Litoral y Prelitoral. Mapas obtenidos de la Agencia Catalana del Agua.* (<http://aca.gencat.cat/ca/laigua/consulta-de-dades/descarrega-cartografica/>)

within this basin, describe the difference between them and discuss its possible cause.

MATERIAL AND METHODS

Study area, sampling sites and data collection

The Tordera River is formed by the main river and several tributary streams (Fig. 1) that drain an area of approximately 900 km² located north-east of Barcelona [see Martín & Maynou (2023) for a description of its geomorphology, climate, hydrology and vegetation].

Onychogomphus forcipatus is more abundant in the middle reaches of the river and tributaries and its flight period is approximately from late May to mid-August. It favours relatively warmer conditions and slower water flows than its congener, *Onychogomphus uncatus* (Charpentier, 1840). The latter lives mostly in the colder, faster and better oxygenated waters of the upper reaches, but also to some extent in the upper sections of the middle reaches where both taxa can coexist (Martín, 1999).

Therefore, we conducted our study in two sites, one in the middle course of the river (site S4; here we use the same identification code as in Martín & Maynou (2023)), and one in the mid-

dle course of the Arbúcies stream, a tributary (site A1). These sites are approximately 7.5 km apart in a straight line (Fig. 1) and their coordinates are UTM ETR S89 461265, 4617825 (elevation: 98 m; slope 0.6 %) and 465055, 4624429 (elevation 123 m; slope 0.9 %) respectively.

At A1 (Fig. 2) the geo- and hydromorphological conditions were rather similar to those at the river site S4 as described in Martín & Maynou (2023) although the flow was somewhat lower. The hydrophyte cover –watercress, *Nasturtium officinale* W. T. Aiton– was limited to the channel margins and the riparian vegetation consisted of annual plants, shrubs and poplar trees (*Populus* sp.). Nevertheless, there were big clearings over the water surface and the channel substrate was mainly sandy with areas including gravel and cobbles in varying proportions. Larval densities, food availability and predators were similar at the two localities during most of the fieldwork period.

Initially, we sampled larvae of *O. forcipatus unguiculatus* monthly at S4 from October 2021 to January 2023 (Martín & Maynou, 2023) and at A1 from February 2023 to January 2024. We performed kick sampling with a D-frame dip net (250 µm mesh) and we sorted the contents on a white-bottomed tray until an appropriate sample size ($\approx$ 20-30 individuals) was attained. We



Figure 2. a) Sampling site A1 at the Arbúcies stream and b) S4 at a subsidiary branch of the Tordera River in July 2023. a) Punto de muestreo A1 en la riera de Arbúcies y b) S4 en un brazo del río Tordera (derecha) en julio de 2023.

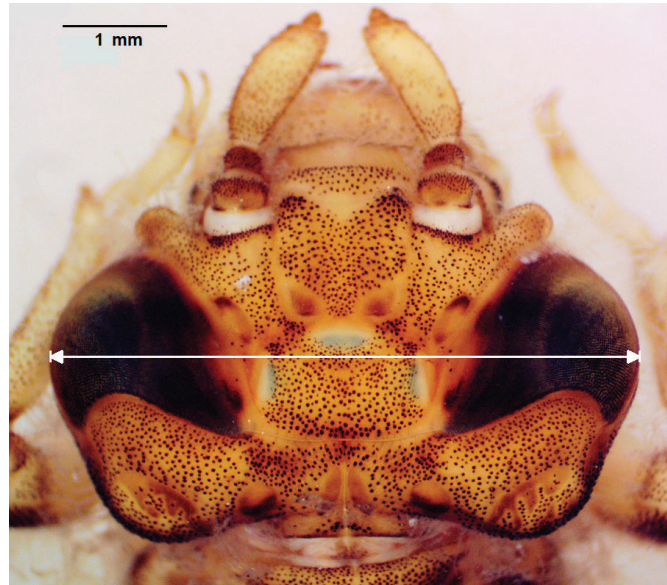


Figure 3. Detail of the head of an *Onychogomphus forcipatus* larva. The length of the arrowed line corresponds to the head width. *Detalle de la cabeza de una larva de Onychogomphus forcipatus. La longitud de la línea con doble flecha es la medida de la anchura de la cabeza.*

identified the collected larvae using the keys in Conesa-García (2021) and measured their head width, including the eyes (Tennessen, 2017) (Fig. 3), with a precision of 0.1 mm under a stereomicroscope at 20x using a calibrated eye-piece graticule.

In October 2023 we realized that there might be differences in the voltinism pattern between S4 and A1 and we decided to monitor water temperatures at both localities as we suspected that temperature differences, if any, might explain the voltinism variation (Corbet, 1999). We recorded them from October 23, 2023 to October 21, 2024 every 15 minutes by means of HOBO® Pendant Temp/Light 64K data loggers (Onset Computer Corporation, Massachusetts, USA) installed near the streambank. In parallel, we extended the sampling of larvae at both locations at approximately two-month intervals until temperature logging was finished to confirm that the voltinism patterns were maintained over time.

Data analysis

To determine the larval growth patterns and the development time we used head-width frequency graphs with data grouped in 0.1 mm class inter-

vals as in Norling (2021).

We calculated the mean daily water temperatures and plotted them over time for A1 and S4 following the HOBO data analysis method developed by Carsten Grupstra (<https://rpubs.com/cgb-grupstra/moorea-hobo-20190314>) with the tidyverse package (Wickham et al., 2019) in R (R Core Development Team, 2024).

We used these mean daily temperatures to calculate the mean seasonal values at the two sites and to draw a box-and-whisker plot to display the temperature distribution trends and differences between seasons and sites. Additionally, we performed a Mann-Whitney U test to check if the seasonal and annual differences between the two sites were significant. All these analyses were carried out using the software PAST ver. 06b (Hammer et al., 2001).

To obtain the degree days, i.e., the number of degrees above the threshold according to McMaster & Wilhelm (1997), we compared the mean daily temperatures with the maximum and minimum values (12°C and 8°C) reported for the lower thermal threshold for larval development for Odonata, i.e., the temperature below which no development occurs (Suhling et al., 2015). Then, we added the daily results to obtain the accumulat-

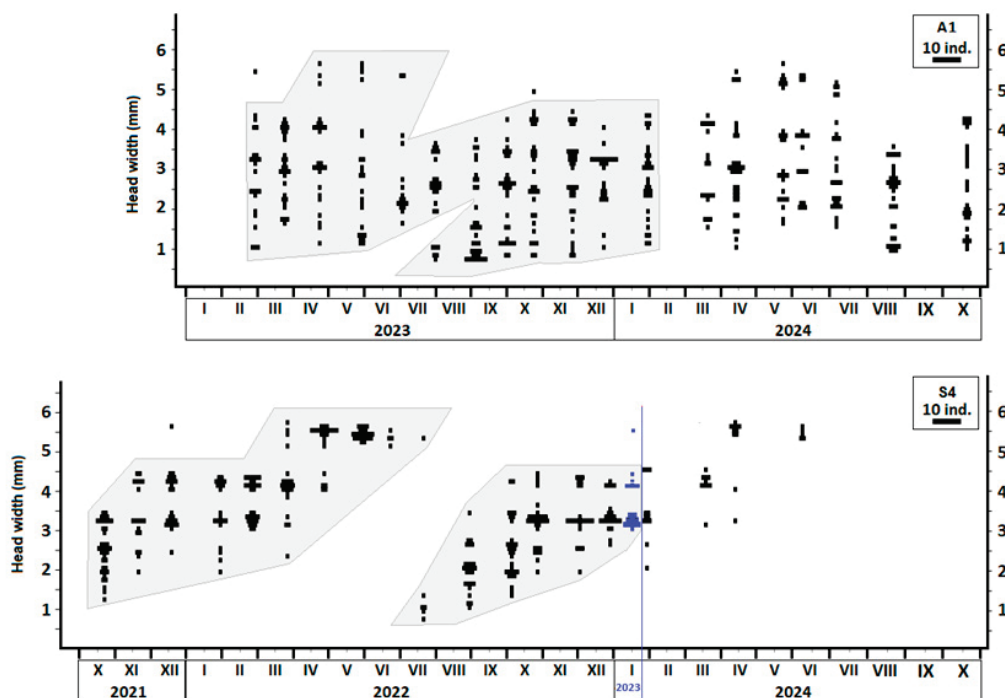


Figure 4. Head-width frequency data for *Onychogomphus forcipatus unguiculatus* at the Arbúcies stream, at the sampling site A1 (above), and at the Tordera main river channel, site S4 (below). While in A1 the graph suggests a mixed voltinism pattern (1–2-year life cycle), it reveals a strictly univoltine life cycle in S4. During 2024, the larval population in S4 dwindled to extinction. Class intervals: 0.1 mm. The grey-shaded areas highlight the differences between both patterns. Regarding the graph for S4, the head-width measurements for 2021 and 2022 have been corrected by a proportion of -3.85% as compared to those published in Martín & Maynou (2023) to compensate for the inaccuracy we discovered in the stereomicroscope we used to take the ones corresponding to the anisopterous species. Since the voltinism pattern was interannually preserved at each site, in order to facilitate comparison between sites we have aligned the graphs by months, sometimes from different years. In the graph for S4, the vertical blue line indicates the approximate date of sampling within January 2023, with the obtained head-width frequency distribution next to it on the left highlighted in blue, and within January 2024 (frequency distribution next to it on the right). *Datos de frecuencia de anchura de la cabeza de Onychogomphus forcipatus unguiculatus en la riera de Arbúcies, en el punto de muestreo A1 (arriba) y en el cauce principal del río Tordera, punto S4 (abajo). Mientras que en A1 el gráfico sugiere un patrón de voltinismo mixto (ciclo de vida de 1-2 años), en S4 revela un ciclo vital estrictamente univoltino. Durante 2024, la población larvaria en S4 disminuyó hasta extinguirse. Intervalos de clase: 0.1 mm. Las áreas sombreadas en gris resaltan las diferencias entre ambos patrones. En relación al gráfico de S4, las medidas de anchura de cabeza de 2021 y 2022 se han corregido en una proporción de -3.85% respecto a las publicadas en Martín & Maynou (2023) para compensar la inexactitud que descubrimos en la lupa binocular que utilizamos para tomar las correspondientes a las especies de anisópteros. Dado que el patrón de voltinismo se conservó interanualmente en cada localidad, para facilitar la comparación entre localidades hemos alineado los gráficos por meses, a veces de diferentes años. En el gráfico S4, la línea vertical azul indica la fecha aproximada de muestreo en enero de 2023, con la distribución de frecuencias de ancho de la cabeza obtenida inmediatamente a la izquierda resaltada en azul, y en enero de 2024 (distribución de frecuencias inmediatamente a la derecha).*

ed degree days for each season and for the entire annual period (October 23, 2023 – October 21, 2024) to test for differences between S4 and A1.

RESULTS

We collected and measured the head width of 1204 larvae, 654 at S4 and 550 at A1. The voltinism patterns of the two populations outlined by the head-width frequency graphs (Fig. 4) show clear differences. At S4 the pattern was typical-

ly univoltine, with practically no indications of coexistence of different year-groups, except in July, but clearly corresponding to successive generations. At A1, though, it was a mixture of uni- and semivoltine, differing from the exclusively univoltine pattern in the greater range of larval sizes over the year indicating the continuous co-occurrence of two generations. These patterns remained constant throughout the sampling periods in each site.

Regarding water temperature monitoring, the

HOBO® installed at S4 started to malfunction on August 20th, 2024 and we could not replace it with a new unit until September 17th. Therefore, we were not able to include the values for the period between these two dates in the temperature analyses.

Water temperatures remained above the maximum and minimum values of the lower threshold

for larval development (Suhling et al., 2015) for most of the year except during the cold period, from mid-autumn to late winter, when the mean daily values fell below the maximum (12°C). This happened earlier and for a longer period in A1 and it was only in this site that temperatures fell below the minimum (8°C) (Fig. 5).

The Mann-Whitney test confirms that the dif-

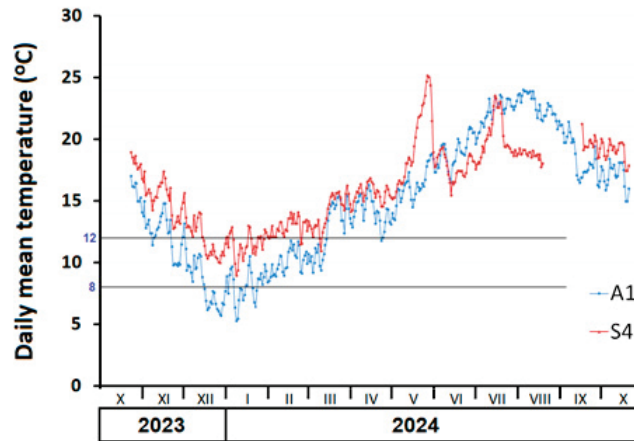


Figure 5. Comparison of mean daily water temperatures measured monthly from October 23, 2023 to October 21, 2024 at A1 in the Arbúcies stream and at S4, in the middle course of the Tordera River. The horizontal lines at 8° and 12° indicate the minimum and maximum values of the lower threshold for larval development (according to Suhling et al. (2015)). The gap in the S4 line between August 20th and September 16th is caused by data loss due to malfunction of the temperature logger at that site between these dates. *Comparación de las temperaturas medias diarias del agua registradas mensualmente desde el 23 de octubre de 2023 hasta el 21 de octubre de 2024 en A1, en la riera de Arbúcies, y en S4, en el curso medio del río Tordera. Las líneas horizontales a 8° y 12° indican los valores mínimo y máximo del umbral inferior de desarrollo larvario (según Suhling et al. (2015)). La discontinuidad en la línea de S4 entre el 20 de agosto y el 16 de septiembre se debe a la pérdida de datos debido al mal funcionamiento del registrador de temperatura en ese lugar entre estas fechas.*

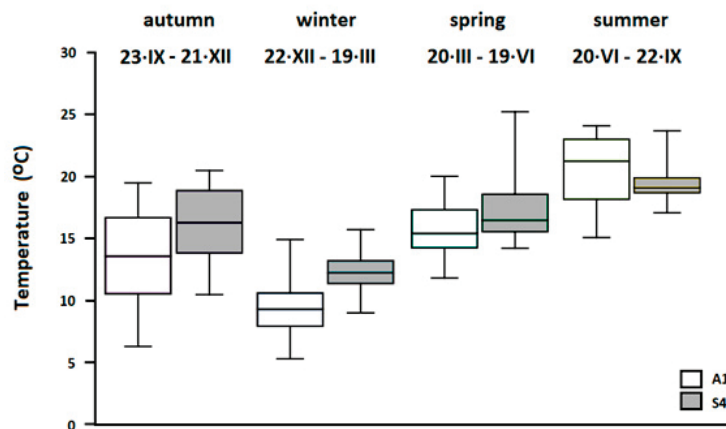


Figure 6. Box and whisker plot showing the seasonal distribution of water temperature readings from October 2023 to October 2024 at site A1 in the Arbúcies stream and S4 in the middle course of the Tordera River. Temperature values between August 20 and September 16 were not included in the calculations due to malfunction of the data logger in S4 during that period. *Diagrama de cajas y bigotes que muestra la distribución de las lecturas de temperatura del agua desde octubre de 2023 hasta octubre de 2024 en el punto A1 en el arroyo de Arbúcies y S4 en el curso medio del río Tordera. Los valores de temperatura entre el 20 de agosto y el 16 de septiembre no se incluyeron en los cálculos debido al mal funcionamiento del registrador de temperatura en S4 durante ese periodo.*

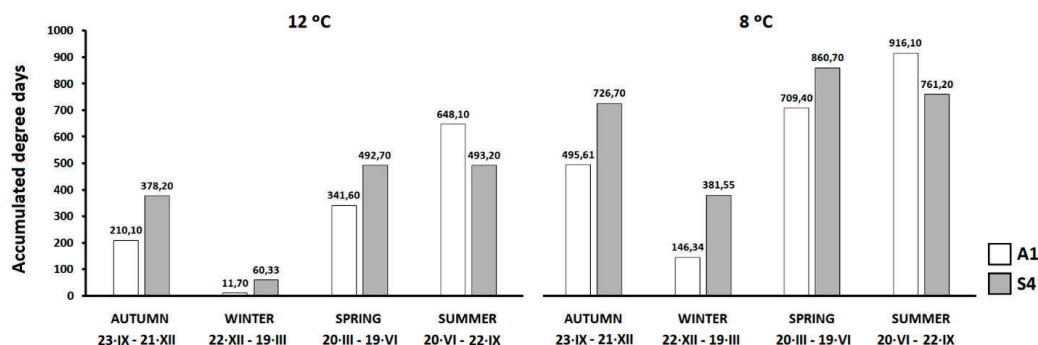


Figure 7. Calculation of accumulated degree days from water temperature readings for each season at A1 in the Arbúcies stream and at S4 in the middle course of the Tordera River for the minimum (8°C; right) and maximum (12°C; left) lower threshold values for larval development. Temperature values between August 20 and September 16 were not included in the calculation due to malfunction of the data logger in S4 during that period. *Cálculo de los grados-día acumulados a partir de las lecturas de temperatura del agua para cada estación en A1 en la riera de Arbúcies y en S4 en el curso medio del río Tordera para los umbrales inferiores mínimo (8°C; derecha) y máximo (12°C; izquierda) para el desarrollo larvario. Los valores de temperatura entre el 20 de agosto y el 16 de septiembre no se incluyeron en el cálculo debido al mal funcionamiento del registrador de datos en S4 durante ese periodo.*

ferences in mean seasonal and annual water temperatures between the two sites (spring: $z=3.874$; summer: $z=7.428$; autumn: $z=5.556$; winter: $z=8.61$; annual: $z=4.154$) were statistically significant ($p<0.0005$). The mean water temperature was higher at S4 than at A1 in autumn (16.2°C vs 13.5°C), winter (12.3°C vs 9.3°C), spring (17.4°C vs 15.8°C) and for the year as a whole (16.1°C vs 14.6°C) but it was lower in summer (19.4°C vs 21.7°C). The box-and-whisker plot (Fig. 6) shows that water temperature values at S4 had, overall, less intra- and inter seasonal dispersion than at A1.

The annual accumulation of degree days above the lower threshold for larval development was 1424 and 2730 at S4 and 1212 and 2267 at A1 for the maximum (12°C) and minimum (8°C) values respectively. Therefore, in total, S4 accumulated between 212 and 463 degree days more than A1. At a seasonal level, S4 accumulated more degree days than A1 in autumn, winter and spring while A1 accumulated more degree days than S4 in summer (Fig. 7).

DISCUSSION

Our results show differences in the voltinism pattern between the *Onychogomphus forcipatus* populations at the Tordera River (site S4) and the Arbúcies stream (S1). The control of voltinism is highly dependent on diapause phenomena. In

dragonfly larvae, the induction and maintenance of diapause and diapause-like states are typically mediated by an interaction of photoperiod and temperature, and diapauses are highly variable in characteristics and duration (Norling, 2021, Table 1, Box 8 and 10). In short-day induced winter diapause, lower temperatures typically increase the critical photoperiod—below which diapause is induced—and also increase the WCS, thus intensifying the general incidence of diapause (Norling, 2021). Together with the direct effects of temperature on growth (Suhling et al., 2015), a difference in the general incidence of diapause was probably the cause of the differences between the life cycles of the two populations subjected to different temperature regimes.

Unlike the exclusively univoltine pattern at S4, the dynamics of the structure of the larval population over time at A1 indicates a mixed uni- and semivoltine life cycle. As expected, the graph for A1 in Figure 4 shows that, while larvae that reached a WCS (stadium F-2 or F-3) before or during winter were able to emerge during the following season, those below these sizes spent another winter in the water. Most likely, larvae from early ovipositions (i.e., late May-June) had plenty of time to grow—they could grow over several months, maybe 4 or 5—, and reach the WCS before winter. When spring came, they entered a fast, emergence-preparing development and emerged during the summer; these larvae, there-

fore, were univoltine. Larvae from later ovipositions had less time to grow before the onset of the cold season and they did not reach the WCS; when they resumed development the following spring, they grew slowly in a weak diapause-like state, neither emerging nor reaching F-0 before next winter. Instead, they spent another winter in the stream, mainly in F-1 and probably some in F-2 and so overlapping with younger larvae. Hence, they accounted for the semivoltine component of the population.

On the other hand, in the middle course of the Tordera River (S4), the absence of intermediate-sized larvae in summer (Fig. 4, below), too small to emerge, and too big to be new recruits, indicates the absence of semivoltinism. The higher number of accumulated degree days (i.e., heat available for growth), especially during autumn and winter (Fig. 7), could have allowed at least small larvae to continue growing if winter diapause was mild or absent until they reached the WCS before the following spring (see Martín & Maynou, 2023). In addition, the WCS is plastic and lowered when milder spring temperatures come early (Norling, 1984, 2021). Apparently, larvae overwintering in the last five stadia in S4 went for emergence during the following season, but in the colder A1 only the last three or four overwintering stadia did so.

Worthy of note are the apparently abnormal water temperature spikes recorded at S4 (Fig. 5) approximately before and after the summer solstice. They might have been caused by a number of temperature-related environmental impacts although it is difficult to attribute them to any in particular. They might be due to water discharges from sewage treatment plants in the surrounding cities and/or from industrial effluents from nearby industrial estates (Urgell, 2008), the effects of which might possibly have been amplified by the reduced flow caused by persistent drought. However, we cannot rule out a malfunction of the Hobo®, which showed signs of failure at the end of August. In any case, as these were temporally restricted occurrences, we do not consider them to have significantly altered the temperature comparison between this locality and A1.

It is also worth mentioning that during the spring and summer of 2024, the larval population

at S4 declined progressively until, at the beginning of summer, there was practically no trace of it left (Fig. 4, below). Concurrently with this, we noticed an increase in the algal coverage of the sand-gravel-cobble channel substrate, an unequivocal sign of eutrophy.

Our finding of univoltinism in the northeastern Iberian Peninsula suggests that in the southernmost edge of the species range, e.g., southern Iberian Peninsula and North Africa, univoltinism may be more frequent than is reflected in the literature. In this sense, regarding some Andalusian populations, Bernal Sánchez (2021) deduced that their life cycle could be univoltine from the fact that they were found in stretches of watercourses that dried up occasionally and that the larvae examined showed a similar level of development.

In northeastern Algeria, Samraoui et al. (2024) described *O. forcipatus unguiculatus* as semivoltine in the Seybouse river, which has similar winter temperatures as the Tordera River (S4). However, their head-width data, when ascribed to the precise sampling dates, demonstrates a virtually identical stadium distribution as in the univoltine S4 population except for the spring sample, where a single most deviant small specimen corresponded to small larvae in the semivoltine cohort in A1. Otherwise, there were no clear indications of semivoltinism and so, apparently, univoltinism was at least common in this locality of the Seybouse.

As previously described, our findings point to water temperature differences between A1 and S4 during the coldest seasons –autumn and winter– (Figs. 5,6,7) as the main driver for the differing voltinism patterns of *O. forcipatus unguiculatus* in these closely located breeding sites. Given the proximity of the sites, it is likely that their populations were linked by dispersion and gene flow leading to a high level of genetic homogenization. Therefore, this suggests a considerable phenotypic plasticity in this species when it comes to responding to local-scale differences in water temperature. Since water temperature may fluctuate over the years, the proportion of individuals that reach the WCS in the first year may vary. Therefore, the populations of the Tordera River would possibly become semivoltine, or partially semivoltine if, for a few years, water temperatures

were lower or the populations of the Arbúcies stream could turn out to be exclusively univoltine if temperatures increased, as is expected under the effects of climate warming.

Müller *et al.* (2000) found a similar response to water temperature in *Gomphus vulgatissimus* (L.) (Odonata: Gomphidae) in Central Europe. Depending on temperature differences, larval development could be finished within two years in warm, shallow rivers or in three or four in cold lakes. In contrast, Lee *et al.* (2022) did not observe divergence in the voltinism pattern between two univoltine populations of the species *Nannophya koreana* Bae, 2020 (Odonata: Libellulidae) in standing water habitats at different elevation with large differences in mean annual water temperatures in South Korea. The cold-water population exhibited a higher growth rate as a compensatory mechanism for the lower water temperature and the shorter length of the growing season. A possible interpretation for the warm-water population is that, to prevent autumn emergence, it displayed a diapause-like regulatory development during late summer, slowed down by high temperatures, but ultimately preparing for winter. This would increase the apparent temperature sum required for development, as suggested by Norling (2021, p. 22).

Overall, we consider that caution should be exercised when assigning a life cycle pattern for a given latitude or geographic region to species with a regulated life cycle (*sensu* Corbet, 1999) because it can be modulated by local differences in environmental variables.

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AUTHOR CONTRIBUTIONS

X.M.: Conceptualization, Investigation, Methodology, Data curation, Writing, Original draft preparation, Reviewing and Editing; R.M.: Conceptualization, Investigation, Methodology, Data curation, Software, Writing, Reviewing and Edit-

ing; U.N.: Conceptualization, Writing, Reviewing and Editing; C.M.: Conceptualization, Resources, Reviewing and Editing, Supervision.

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