

Slow and steady wins the race: Life cycle and seasonal regulation of *Gomphus lucasii* (Odonata: Gomphidae)

Boudjéma Samraoui^{1,2,5}, Laïd Touati^{1,3} & Farrah Samraoui^{1,4}

¹ Laboratoire de Conservation des Zones Humides, Université 8 Mai 1945 Guelma, Algeria

² Department of Biology, University of Annaba, Annaba, Algeria

³ Department of Biology, University of Constantine, Constantine, Algeria

⁴ Department of Ecology, Université 8 Mai 1945 Guelma, Guelma, Algeria

⁵ Corresponding author, bsamraoui@gmail.com;
ORCID ID: 0000-0002-0608-9021

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Abstract. We investigated the emergence and life cycle of the endangered Maghrebien endemic *Gomphus lucasii* at the Seybouse River in north-eastern Algeria. Starting in mid-April, their emergence, typical of spring species, was highly synchronized and was achieved within two to three weeks. EM₅₀ was reached in three days. Larval sampling indicated that the synchrony was achieved through larvae overwintering in the F-0 stage. Noteworthy was the concomitant presence of a junior cohort throughout the year demonstrating that the species completes a generation in two years. Thus, contrary to what has been reported previously, we argue that *G. lucasii* is a semivoltine species with a 'slow' developmental rate congruent with its distribution in high-risk permanent habitats. This finding has important conservation implications for this threatened endemic species which is facing severe anthropogenic pressures in the context of global changes.

Further key words. Dragonfly, Anisoptera, voltinism, North Africa, Algeria

Introduction

Knowledge of voltinism, the number of generations completed in a year, is essential to identify factors driving seasonal regulation in Odonata and may explain the successful colonization of temperate and higher latitudes areas by these warm-adapted insects (PRITCHARD 1982; NORLING 1984; CORBET 1999; CORBET et al. 2006). Preliminary studies of emergence characteristics and larval development of Odonata have shed considerable light on life history patterns and allowed the classification of various taxa into spring

or summer species (CORBET 1964). Initially, Odonata undergoing a diapause in the final larval instar and emerging synchronously are referred to as spring species whereas those lacking a diapause in the final larval instar display a poorly synchronized emergence and are termed summer species since their protracted emergence period stretches over the summer months (CORBET 1954).

The division between spring and summer species, though extremely helpful in providing insight into mechanisms of seasonal regulation, should not be adhered to rigidly (PAULSON & JENNER 1971; CORBET 1999). For instance, additional adaptations are found in Mediterranean or tropical species (KUMAR 1972; SAMRAOUI et al. 1998; AGÜERO-PELEGRIN et al. 1999). These special cases have prompted an improvement to the initial classification which now divides the temperate odonate life cycle into three types. The first two types apply to spring and summer species, respectively and a third type refers to a subset of summer species exhibiting an obligatory univoltine cycle (CORBET 1999; CORBET & BROOKS 2008).

A landmark in the investigation of factors driving seasonal regulation of Odonata was the discovery that seasonal change in photoperiod could act as a clue to larval development (CORBET 1955, 1956). Further work indicated that larval photoperiodic responses acting in concert with temperature provide the framework for seasonal regulation (NORLING 1984; CORBET 1999).

Studies of the ecology of North African Odonata have been initiated in the early 1990s and they quickly indicated a latitudinal difference in their life histories shared by southern European species (SAMRAOUI et al. 1993, 1998; MUÑOZ-POZO & FERRERAS-ROMERO 1996; SAMRAOUI 2009). Based on an extensive survey of Algerian wetlands, a classification based on the adult flying season was proposed for North African Odonata (SAMRAOUI & CORBET 2000). However, despite preliminary studies (ZEBSA et al. 2014, 2015; HAMZAOUI et al. 2015; KORBAA et al. 2018), knowledge of the ecology of Algerian Gomphidae is still lagging far behind other aquatic taxa mainly because, for more than a decade, mountain streams and rivers were mostly inaccessible for security reasons.

Within the Mediterranean basin, the Maghreb hosts two endemic gomphids, *Onychogomphus boudoti* Ferreira, 2014, and *Gomphus lucasii* Selys, 1849. The former is confined to a small area in the Middle Atlas, Moroc-

co (FERREIRA et al. 2014) and its status (CR) is a cause of a serious concern (FERREIRA 2016). *Gomphus lucasii* is restricted to Algeria and Tunisia (DUMONT 1977; SAMRAOUI & MENAÏ 1999; JÖDICKE et al. 2000) and is considered Vulnerable (VU) on the Mediterranean (RISERVATO et al. 2009) and North African IUCN Red Lists (SAMRAOUI et al. 2010). Because of its vulnerable status, the species' ecology has attracted some attention and, recently, ZEBBA et al. (2014) investigated its life cycle and claimed that it was a univoltine species. Furthermore, based on extrapolation, they asserted the species to be more abundant than previously assessed (RISERVATO et al. 2009; SAMRAOUI et al. 2010).

To address these questions that bear important repercussions on the conservation of an endemic threatened taxon, we conducted a study with a two-fold objective: i) investigate the emergence pattern and elucidate the life cycle of *Gomphus lucasii* and ii) infer and discuss how this life cycle pattern could be regulated.

Material and methods

During two years, we collected exuviae at a single station (Chihani, Seybouse River, north-eastern Algeria) from 1st April to 15th August. Both intermittent (2015) and daily (2016) sampling of exuviae was carried out. Also, monthly sampling of larvae was performed at two stations of the Seybouse River (Chihani, elevation 20 m a.s.l. and Cheniour, 640 m a.s.l.). In parallel, over a hundred localities distributed over various Algerian rivers and streams were also sampled to provide additional information on the distribution and abundance of *Gomphus lucasii*. The results of this additional survey will be treated elsewhere. Larvae were collected with a hand net (1 mm mesh size) via kick sampling and sweeping all types of microhabitats. Samples were stored in 70 % ethanol, identified and measured (head width and body length with accuracy of 0.1 mm) in the laboratory.

A logistic curve $\frac{A}{1+e^{-K(\text{date}-T)}}$ was fitted to the emergence curves with parameters (A = curve's maximum value, K = logistic growth rate, and T = x-value of the sigmoid mid-point) derived by a process of iteration. To evaluate synchronization of emergence, we measured EM_{50} , the time in days spent between the start of emergence and when 50 % of the annual population has

emerged. A generalized linear model (GLM) with Gaussian error distribution was carried out to test whether date, year and sex could account for total length or head width. Model validation was performed to check the robustness of each model. All statistical analyses were carried out using R (R DEVELOPMENT CORE TEAM 2019).

Results

A total of 89 exuviae and 65 larvae were collected during the study period. Because of the small sample size and no apparent differences in development between the two sampling sites, larval data were combined. Preliminary, as yet unpublished analysis of the larval survey confirmed that *Gomphus lucasii* is sparsely distributed across its range. The additional survey also identified multiple stressors (pollution, sand extraction, dam construction) affecting lotic hydrosystems across Algeria. For example, starting from 2017, the Chihani locality was completely degraded by sand and gravel extraction for road building and the crossing of a pipeline across its shores.

Emergence

In the first study year, emergence started on 23-iv-2015 and ended by 15-v-2015, thus lasting 22 days. The following year, emergence started earlier on 18-iv-2016 and was completed by 29-iv-2016, lasting 11 days. In both years, the iteration process to determine the parameters of the logistic equation converged quickly (2015: $A = 16.50$, $K = 0.68$, $T = 26.99$, $R^2 = 0.99$; 2016: $A = 71.60$, $K = 0.38$, $T = 20.41$, $R^2 = 0.99$) and the emergence curve could be modelled by a logistic curve (Fig. 1). In 2015, EM_{50} was achieved within four days (Table 1). Similarly, in 2016, EM_{50} was brief and completed in two days (Fig. 2).

In both years, there was a temporal separation between the mass emergence of *G. lucasii*, which started first and ended by the time the extended emergence of the sympatric *Onychogomphus costae* Selys, 1885, kicked off. The emergence seemed to proceed at night as by early morning only a few stragglers could be noted lingering. Numerous bird tracks made it clear that the river banks were regularly patrolled and the frequent sights of Little Egret *Egretta garzetta*, White Stork *Ciconia ciconia*, and Common Sandpiper *Actitis hypoleucos* confirmed that the diurnal emergence of the laggards was a perilous enterprise.

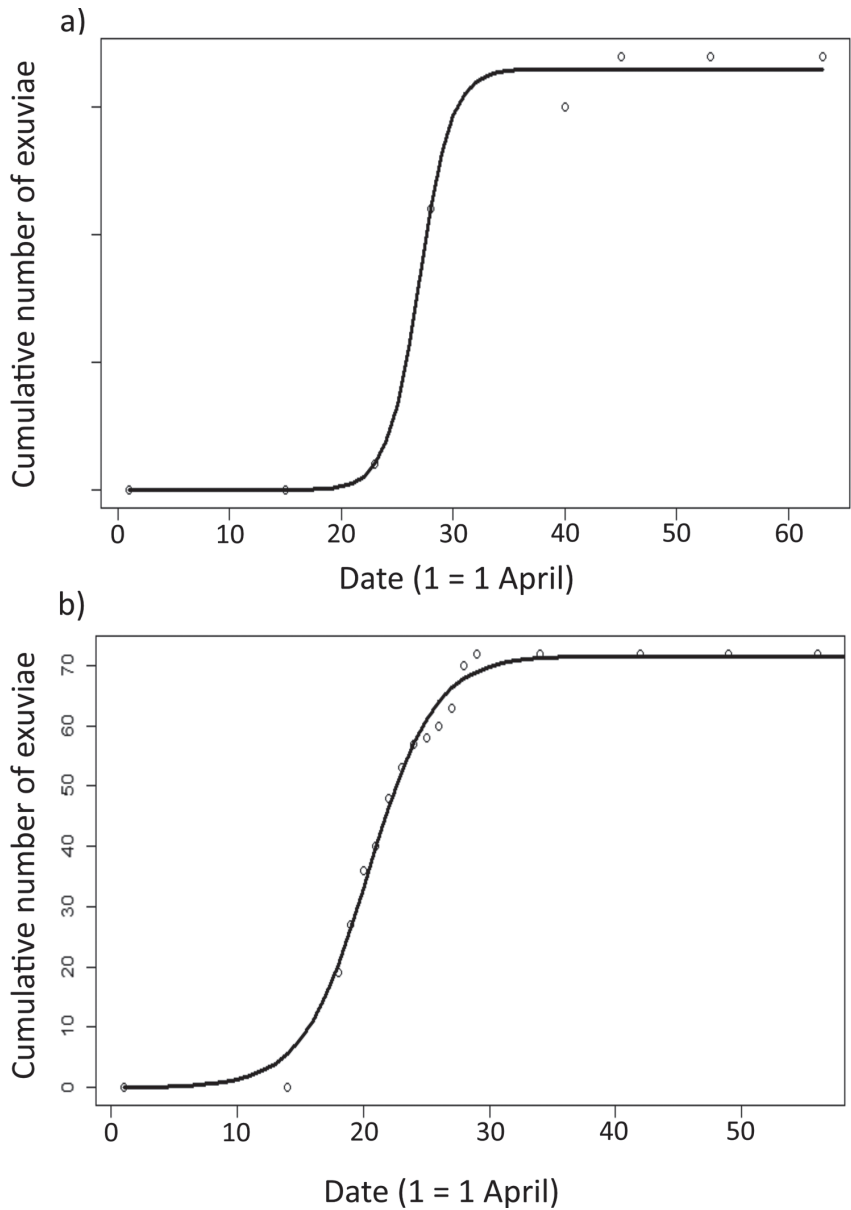


Figure 1. Cumulative number of exuviae of *Gomphus lucasii* sampled at the Seybouse River, north-eastern Algeria, with a fitted logistic curve: a – 2015, b – 2016.

Table 1. Start and duration of the emergence curves of *Gomphus lucasii* at the Seybouse River in north-eastern Algeria, based on exuviae. Values of EM_{50} have been derived using the difference between the T parameter of the fitted logistic curve and the onset of emergence.

Year	Start	End	Date (50 %)	50 % [d] (total emergence period)	n
2015	23-iv	15-v	26-iv	3.99 (22)	17
2016	18-iv	29-v	20-iv	2.41 (11)	72

Emergence support

Overwhelmingly, *G. lucasii* emerged over the water, used plants as support (96 %), and only rarely adopted stones or the shore (4 %). The saltmarsh bul-rush *Scirpus maritimus* was the dominant plant support, followed by *Typha angustifolia*, *Paspalum distichum* and *Tamarix gallica*.

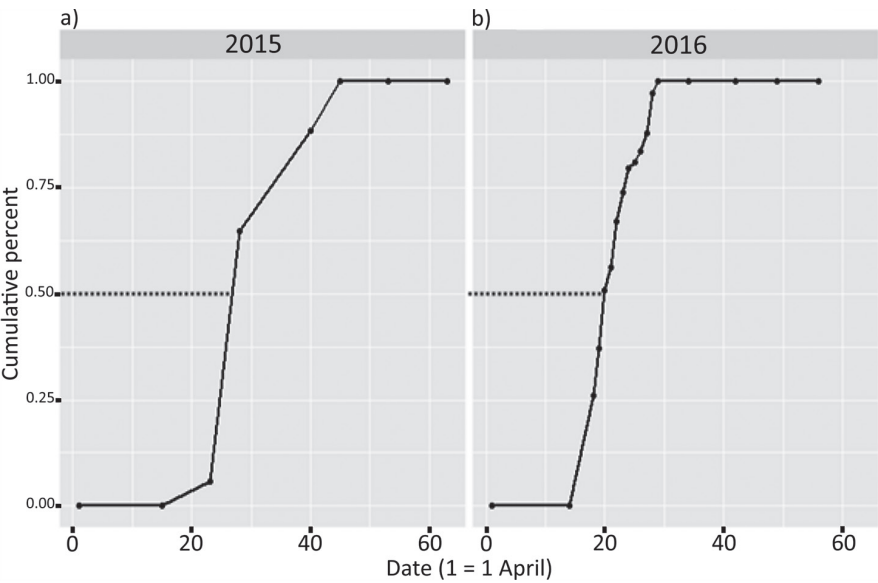


Figure 2. Cumulative percent of emergence curve of *Gomphus lucasii* based on exuviae sampled at the Seybouse River, north-eastern Algeria. EM_{50} values expressed in days, represent the period between the onset of emergence and when 50 % of the annual population has emerged.

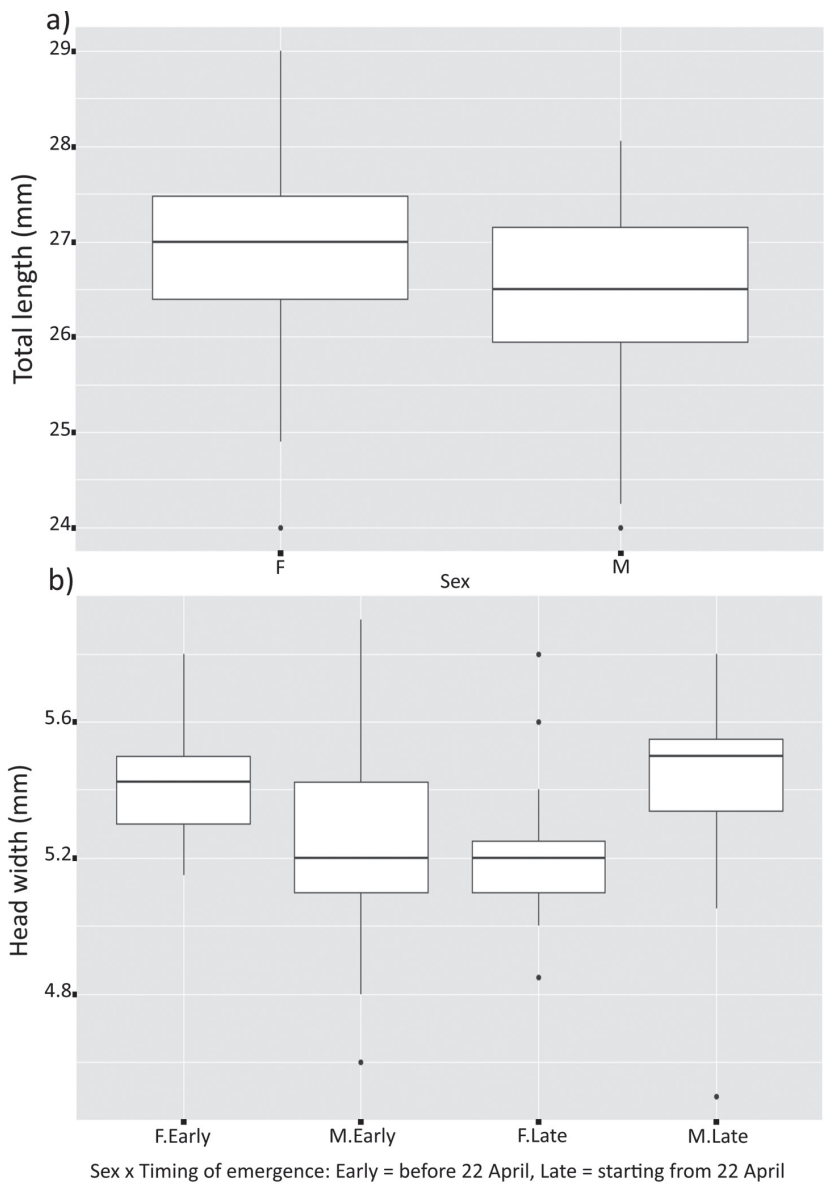


Figure 3. Boxplots of total length of *Gomphus lucasii* exuviae sampled at the Seybouse River, north-eastern Algeria, according to sex (a) and head width according to sex and timing of emergence (Early vs Late).

Table 2. Number of exuviae of *Gomphus lucasii* and their sex-ratio sampled at the Seybouse River, north-eastern Algeria, during the study period.

	2015	2016	Total
Number of exuviae	17	72	89
Number of males	7	39	46
Males [%]	0.41	0.54	0.52

Table 3. GLM estimates of total length and head width of *Gomphus lucasii* exuviae sampled at the Seybouse River, north-eastern Algeria.

Parameter	Estimate	s.e.	t-value	P
Total length (n=83)				
Intercept	26.91	0.16	163.91	2 e-16
Sex	0.41	0.23	1.82	0.07
Head width (n=68)				
Intercept	6.05	0.29	21.07	2 e-16
Sex	1.19	0.40	2.98	0.004
Date	0.03	0.01	2.50	0.015
Sex × Date	0.05	0.02	2.94	0.005

Sex ratio of exuviae

The timing of emergence was not associated with sex (One way ANOVA: $F_{1,68} = -0.30$, $p = 0.76$) and the overall sex ratio of exuviae was relatively unbiased (52 % in favour of males). Differences between years were not significant (Fisher's Exact Test for count data: $p = 0.64$) (Table 2).

Body size of exuviae

Exuviae length did not differ between years (One-way ANOVA: $F_{1,81} = 1.34$, $p = 0.25$) so they were merged into a single data set. A GLM model indicated that sex had a non-significant effect on length ($p = 0.07$) with females being marginally longer than males (Table 3, Fig. 3a). Conversely, head width was shown to be significantly dependent on the interaction between the date of emergence and sex. Early females had a larger head width than early males and late females while late males had a larger head width than early males and late females (Table 3, Fig. 3b).

Life cycle

Egg development was direct with the smallest larvae (total length <10 mm), indicative of hatching, first appearing in June. Head width and total body length were sufficient to distinguish the last four stadia which exhibited no overlap (Fig. 4). Despite the limited larval samples in winter and spring, a clear pattern emerged with the larval size distribution exhibiting a bimodal pattern throughout the year (Fig. 5). The only exception was the summer period where various stadia (F-1, F-2, F-3) could be found. The last stadium was reached in autumn and these F-0 larvae passed their second and last winter in diapause before the onset of emergence in mid-spring.

Discussion

Although our survey was by no means exhaustive, our results indicate that *Gomphus lucasii* is certainly neither widespread nor abundant and confined

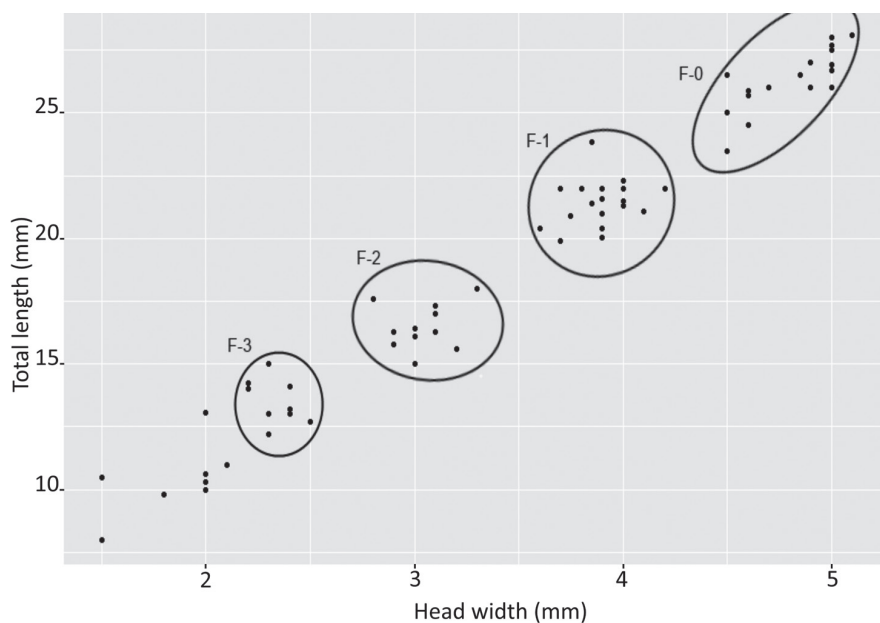


Figure 4. Relationship between total length and head width of *Gomphus lucasii* larvae sampled at the Seybouse River, north-eastern Algeria. Ellipses and circles have been used to delineate the last four stadia (F-0 to F-3).

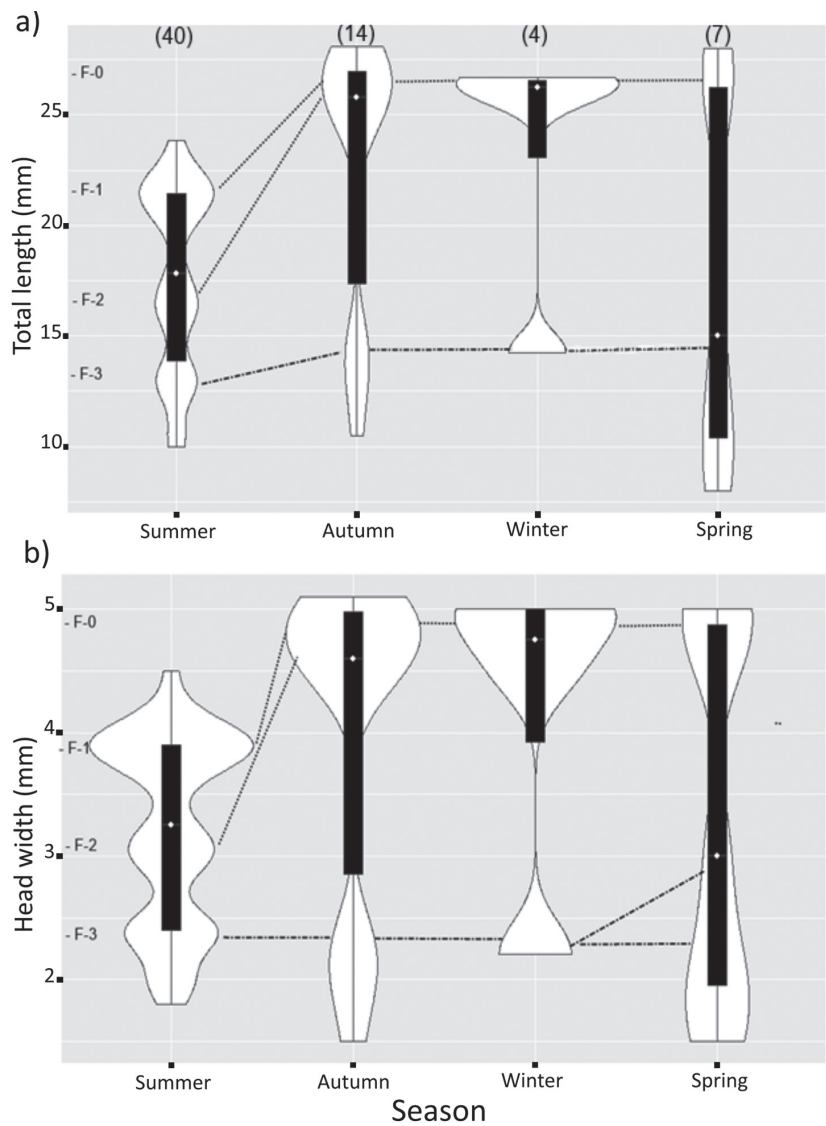


Figure 5. Size-frequency distribution plot of *Gomphus lucasii* larvae sampled at the Seybouse River, north-eastern Algeria. White dots within boxplots indicate median values: a) body length, b) head width. Dotted lines indicate the development of the F-1 and F-2 stadia into F-0 stadium whereas dashed lines suggest arrested or minimal development of F-3 stadium larvae. The sample size is given in parentheses.

to permanent habitat inhabited by Algerian Barb, *Luciobarbus callensis*, or other congeners. The flight period of the species is brief, restricted mainly to spring (May and June) but by combining data of larvae and exuviae, our study was able to provide a useful confirmation of the precarious status of this threatened endemic. The Seybouse River remains, undoubtedly, the location where the species is most frequent. Yet, to our knowledge, the distribution of *G. lucasii* along this river is patchy and over the last ten years the population has never been abundant. Besides, multiple anthropogenic stressors have been affecting the Seybouse River and many stations, where the species was previously known, have now been severely degraded and the populations have gone extinct.

In both years, the emergence period of *G. lucasii* was short, limited to a couple of weeks in mid-spring. Indeed, half of the population emerged within a matter of a couple of days. This pattern is typical of spring species like *Anax imperator* Leach, 1815, where 50 % of the annual emergence occurs in the first three days (CORBET 1957). The emergence duration was also shorter (11–22 days) compared to one month as reported by ZEBBA et al. (2014) for the same species. Our recorded values of EM_{50} (2–4 days) are also substantially shorter than the ten days recorded by the same authors. However, striking differences in EM_{50} within and between habitats have also been described for *Onychogomphus uncatus* (Charpentier, 1840) (SUHLING 1995).

No differences were found between the timing of emergence of the sexes and, overall, the sex ratio of *G. lucasii* at emergence was relatively unbiased, congruent with results from a comprehensive analysis of exhaustive exuviae collections (CORBET & BROOKS 2008). For the majority of individuals, emergence occurred vertically, using plants as support. Only on rare occasions, stones were used to support the final metamorphosis even though *Gomphus* is known to be an exception among Odonata in using horizontal emergence support (CORBET & BROOKS 2008).

Larval body length at emergence was found to be marginally linked to sex with females slightly bigger than males. However, body length did not vary with time as reported by ZEBBA et al. (2014). In contrast, head width exhibited a complex pattern with a significant sexual dimorphism throughout the emergence period. Females had larger head widths than males in the initial stage of emergence before the pattern was reversed. Although the causes of

such reversal are unclear, the timing of emergence and body size at emergence are two key fitness components with larval carry-over effects to adult fitness (STOKS & CORDOBA-AGUILAR 2012) so their importance cannot be overstated.

One explanation of intraspecific size differences is based on differential larval development when a supernumerary moult is interpolated late in larval life (CORBET 1999). Another explanation put forward involves the timing and the developmental stage of the overwintering stadium (AOKI 1993). Other authors (SUHLING 1994; ANHOLT 1990) have demonstrated that environmental heterogeneity in distinct microhabitats may also be responsible for such differences in head width. Finally, character displacement and niche shift may also influence allometric growth (ROBINSON & WELLBORN 1987). In Odonata, sexually mature females are generally larger and/or heavier than males (ANHOLT et al. 1991; THOMPSON & FINCKE 2002) and many functional hypotheses have been put forward to explain this female-biased sexual size dimorphism (CROWLEY & JOHANSSON 2002; SERRANO-MENESES et al. 2007). However, whether and how body size correlates with fitness remains a controversial issue (SOKOLOVSKA et al. 2000; THOMPSON & FINCKE 2002).

In our study, data indicated an early emergence and a high degree of synchronicity, implying that the senior cohort overwinters at the F-0 stage. This latter was reached by early autumn. These larvae, as is found in typical spring species, were set to overwinter in the final stadium before emerging in early spring. Additionally, the presence of at least two cohorts in autumn, winter, and spring rules out the likelihood of a univoltine life cycle and points unambiguously to a semivoltine life cycle.

Thus, our results are not congruent with the conclusions of ZEBBA et al. (2014), who asserted that *G. lucasii* completes a generation within a single year. In addition, the authors reported an apparent absence of larvae during the summer months (July and August) and a sudden presence of F-0 larvae in October. These contradictory findings and the factual presence of small larvae throughout the year suggest inadequate sampling. Besides, the presence of F-2 larvae in April in the authors' samples, before emergence, is a conclusive clue against a univoltine life cycle. Indeed, diapause plays a key

role in synchronizing emergence in spring species (CORBET 1999) and because of the explosive nature of this emergence, which is achieved in two or three weeks, there is simply no time for the smaller larvae to reach the final stadium and emerge with the senior cohort.

We found no evidence of life-history plasticity along an altitudinal gradient or an alternative life cycle like that of another spring species, *Gomphus vulgatissimus* (Linnaeus, 1758) (HORVÁTH 2012), which may extend the duration of its emergence (FARKAS et al. 2012) or complete its larval development in two, three or four years (MÜLLER et al. 2000). Thus, larval development of *G. lucasii* at the Seybouse River did not allow for a generation to be completed within a year and was similar to that of another semivoltine gomphid, *Gomphus pulchellus* Selys, 1840, which also exhibits an early mass emergence, typical of a spring species (MÜLLER & SUHLING 1990; FERRERAS-ROMERO & GARCÍA-ROJAS 1995).

At present, *Paragomphus genei* (Selys, 1841), remains the only exception among Palaearctic gomphids that may exhibit a univoltine (TESTARD 1975) or even a bivoltine (JÖDICKE 2001; WEIHRAUCH & WEIHRAUCH 2003) life cycle. All other known Palaearctic gomphids that have been investigated thus far take at least two years to complete a single generation (CORBET et al. 2006). The 'fast' life-history strategy (SIH 1987) exhibited by *P. genei* agrees well with its occurrence in fishless, temporary habitats and it contrasts sharply with the 'slow' life style of a large-bodied burrower like *G. lucasii* that occupies the other end of the predator-permanence gradient (WELLBORN et al. 1996; JOHANSSON 2000; JOHANSSON & SUHLING 2004; MCCAULEY 2008).

We can infer that the life cycle of *G. lucasii* is probably regulated at the larval stage by a combination of seasonally correlated cues such as temperature and photoperiod (CORBET 1999). One likely framework for the seasonal regulation of the larvae of *G. lucasii* is the model proposed by NORLING (1984), which involves a two-phase photoperiodic reaction interacting with temperature. The response of overwintering larvae to the photoperiod (diapause or fast development) relies on larvae attaining a 'winter critical size' (NORLING 1984). In the case of *G. lucasii*, any stadium higher than F-3 in

summer appears to develop towards reaching the final stadium in autumn whereas smaller larvae appear to enter into a long-day diapause with minimal growth, if at all, until the onset of spring. This long-day diapause may prevent the junior cohort from emerging at an unfavourable period. However, experimental data are needed to provide more insight into this hypothetical mechanism.

The Seybouse River is one of the very few permanent rivers in North Africa and its species richness owes considerably to the fact that it provides a permanent flow to a range of aquatic species whose larval growth and development require water during the arid Mediterranean summer. Unfortunately, permanent freshwater habitats in North Africa are experiencing considerable loss and degradation due to anthropogenic activities (GARCIA et al. 2010; MORGHAD et al. 2019; BENSLIMANE et al. 2019). Despite the rapid biodiversity erosion and under the looming pressure of climate change, the Seybouse River can still qualify as a Key Biodiversity Area (LANGHAMMER et al. 2007) but an Integrated River Basin Management needs to be implemented to ensure among other steps that this management guarantees the provision of an 'environmental flow' along the whole watercourse (DYSON et al. 2003) and develop effective conservation actions.

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