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Life cycle, nymphal feeding and secondary production of *Dinocras cephalotes* (Plecoptera) in a Mediterranean river

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Summary. Some aspects of the life history of a population of *Dinocras cephalotes* inhabiting a Mediterranean river in Southern Spain were studied over a year (2012–2013). The life cycle of this population seems to be semivoltine, of approximately two years of duration, and with an asynchronous egg hatching period. The comparison of these data with those of an unpublished study carried out in the same population almost a decade before (2004–2005) shows the existence of no differences between years. The nymphal feeding study revealed that the main prey of these organisms are Chironomidae, Psychomyiidae and Baetidae, but some of them, usually the smallest, also had non-animal matter in their guts, mainly detritus, coarse particulate organic matter and algae. So, an ontogenetic shift in feeding was detected. This feeding confirms broadly what was already reported in previous studies in the same and other populations. Finally, and for the first time for this species, the secondary production was estimated. Due to differences in hatching, and so development, among nymphs, annual secondary production was calculated both assuming a CPI of 20 months and a CPI of 14 months. In both cases this value was relatively high, 2854.46 and 4077.80 mg DW m⁻² year⁻¹, respectively. These results were compared with those of other predators, and particularly with a stonefly predator with a similar life cycle and from a nearby temporal river.

Résumé. Cycle de vie, régime alimentaire de la nymphe et production secondaire de *Dinocras cephalotes* (Plecoptera) dans une rivière méditerranéenne. Certains aspects de l'histoire naturelle d'une population de *Dinocras cephalotes* d'une rivière méditerranéenne du sud de l'Espagne ont été étudiés durant un an (2012–2013). Le cycle de vie de cette population semble être semivoltine, avec une durée d'approximativement deux ans, et avec une période asynchrone d'éclosion. La comparaison de ces données avec celle d'autre étude non publiée accomplies dans la même population près d'une décennie plus tôt (2004–2005) ne montre pas de différence entre ces années. L'étude du régime alimentaire des nymphes révèle que leurs proies principales sont des Chironomidae, Psychomyiidae et des Baetidae. Toutefois certaines de ces nymphes, en général les plus petites, avaient aussi de la matière non-animale dans leur tube digestif, surtout des détritiques, des parcelles organiques grossières et des algues. On a donc observé un changement ontogénique d'alimentation. Ce régime alimentaire confirme largement ce qui était déjà constaté lors d'études antérieures sur cette population et d'autres. Enfin, et pour la première fois pour cette espèce, on a pu estimer la production secondaire. En raison des différences d'éclosion, et donc de développement des nymphes, la production secondaire annuelle a été calculée en adoptant un CPI de 20 ou de 14 mois. Dans les deux cas, cette valeur a été relativement haute, soit 2854.46 et 4077.80 mg DW m⁻² year⁻¹ respectivement. Ces résultats ont été comparés avec ceux d'autres prédateurs et particulièrement avec une perle de cycle de vie identique et d'une rivière temporaire voisine.

Keywords: life history; Perlidae; Southern Spain; stonefly

The stonefly *Dinocras cephalotes* (Curtis 1827) is the most widely distributed European Perlidae, found from Southern Spain (Cádiz) and Southern Italy (Sicily) (Sánchez-Ortega et al. 2003; Fochetti & Tierno de Figueroa 2008) to Northern Fennoscandian (Lillehammer 1974; Erkinaro & Erkinaro 2003).

Considering its ecological requirements regarding egg development, *D. cephalotes* has always been considered and reported as a warm stenotherm species (Elliott 1989; Zwick 1996a; Sand & Brittain 2001).

However, other factors seem to be important in shaping its autoecology: for instance, in Spain its altitudinal range spans from 40 to 2800 m asl and in Italy from 60 to 1650 m asl (Tierno de Figueroa, Sánchez-Ortega, et al. 2003; Fochetti & Tierno de Figueroa 2008). Together with the above-reported wide latitudinal distribution, from 36° to 70° N, its broad altitudinal range makes *D. cephalotes* more euryecious than previously thought. That is why Graf et al. (2009) reported it as eurythermous.

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Besides its wide latitudinal and altitudinal distribution and its relatively euryecious character, *D. cephalotes* is an important ecological element of the European rivers for some other reasons: it is a top predator within the macroinvertebrate communities, its large size (mature nymphs can reach more than 3 cm) and relative high abundance make it an important prey for carnivorous fishes such as the brown trout, and adults constitute a respectable resource for terrestrial predators such as spiders or birds. Hence, many studies have been conducted to understand the biology of this species.

One of the most studied aspects of the biology of *D. cephalotes* throughout its geographical range is its life cycle (Hynes 1941; Brinck 1949; Frutiger 1987; Huru 1987; Frutiger & Imhof 1991; Sánchez-Ortega & Alba-Tercedor 1991; Sand & Brittain 2001; Iannilli et al. 2002). Life cycle length seems to vary from two to six years. This variability is mainly due to environmental factors (principally water temperature) but also to the difficulty in properly inferring its real duration: it is sometimes difficult to distinguish different cohorts because of the sexual dimorphism in size (Sand & Brittain 2001). In addition, the demonstrated existence of plurimodal hatching of *D. cephalotes* eggs (Zwick 1996b) contributes to blurring the understanding of the real length of its life cycle.

Nymphal feeding habits have been also well studied (Malmqvist & Sjöström 1980; Berthélemy & Lahoud 1981; Lillehammer 1988; Lucy et al. 1990; Elliott 2000, 2003; Bo et al. 2007, 2008; Gallo et al. 2010; López-Rodríguez et al. 2012) because of the important role of nymphs as top-predator within the lotic macroinvertebrate food web, as previously noted. It turns out that *D. cephalotes* behaves as a more generalist predator and it is able to assimilate a wider trophic resource spectrum than other Perlids with which it coexists. This could be one of the reasons why this species has a wider global distribution.

On the other side, the knowledge of the secondary production of *D. cephalotes* is so far inexistent, despite being an important parameter to evaluate the ecological role of a species in its biocoenosis (Benke 1993).

In the present work, we study the life cycle, nymphal feeding and secondary production of a *D. cephalotes* population inhabiting a Mediterranean river in Southern Spain. We compare the results of this one-year study with our own unpublished data on the life cycle of this same population from a study carried out almost a decade ago. We also compare our nymphal feeding results with those previously published for this species in the same river, and those of the secondary production analysis with data of other stonefly predator from a nearby area.

Material and methods

Nymphs of *D. cephalotes* were collected in Castril River (Sierra de Castril, Granada, South Iberian Peninsula; 37°52'37.6"N, 2°



Figure 1. Map of the Iberian Peninsula showing the study area.

45°26.1"W; 1040 m asl; Figure 1). Castril River is a tributary of the Guadalquivir River, and exhibits a limestone substrate composed by cobbles and gravel.

Nymphs were collected with a Surber sampler (area = 0.1 m², 250 µm mesh size). We took six samples during each sampling event for the secondary production calculation as well as additional samples to have a higher number of nymphs for the life cycle and feeding studies; they were preserved in 70% ethanol and brought to the laboratory. Samplings were carried out monthly from V.2012 to V.2013. All the macroinvertebrates present in the samples were also preserved in 70% ethanol, brought to the laboratory and identified to characterize the community (Table 1). For the comparison of the life cycle of *Dinocras cephalotes*, we used nymphs collected monthly in the same site from VII.2004 to VII.2005.

Water temperature was hourly recorded by a datalogger (iBCod, Eclo, 0.01°C accuracy; Eclo, Portugal) placed in the riverbed during the whole sampling period. The water at our sampling station was characterized (during the study period) by very constant mean daily temperatures, ranging only from 8 to 16°C (Figure 2).

Conductivity and pH were measured monthly with a multi-parametric probe (VWR Symphony, VWR International Eurolab S.L., Llinars del Vallès, Barcelona, Spain), and discharge (m³ s⁻¹) was also monthly measured with a propeller meter (Global Water Mod. FP101, Global Water Instrumentation, Gold River, CA, USA) *in situ* during each sampling event. Conductivity ranged from 209.10 to 243.00 µS cm⁻¹ (mean = 220.38, SD = 11.20, n = 13), pH ranged from 8.44 to 8.87 (mean = 8.69, SD = 0.12, n = 13) and discharge ranged from 0.41 to 4.51 m³ s⁻¹ (mean = 1.71, SD = 1.48, n = 13).

To describe the life cycle we measured, during the days following each sampling event, the pronotum width of every collected specimen with the micrometer of a binocular microscope (10×). We distributed nymphs in 0.5 mm length size classes and represented the life cycle by means of size–frequency graphs with the FiSAT II software (version 1.2.0, www.fao.org/fi/statist/fisoft/fisat/index.htm).

We used the size–frequency method to evaluate secondary production because nymphs of different size classes were present at the same time (Hynes & Coleman 1968; Hamilton 1969; Benke 1979, 1993; Benke & Huryn 2006). We applied a

Table 1. Macroinvertebrate taxa collected during the study period (2012–2013).

Taxa	
Oligochaeta	Lumbricidae Lumbriculidae
Hirudinea	
Ephemeroptera	Baetidae <i>Baetis</i> sp. Ephemerellidae <i>Serratella</i> sp. Ephemeridae <i>Ephemera</i> sp. Caenidae <i>Caenis</i> sp. Heptageniidae <i>Epeorus</i> sp. <i>Ecdyonurus</i> sp. <i>Rithrogena</i> sp.
Plecoptera	Perlidae <i>Perla</i> sp. <i>Dinocras</i> sp. <i>Leuctra</i> sp.
Odonata	Leuctridae <i>Leuctra</i> sp. Gomphidae <i>Onychogomphus</i> sp.
Tricoptera	Brachycentridae <i>Micrasema</i> sp. Lepidostomatidae <i>Lasiocephala</i> sp. Sericostomatidae <i>Sericostoma</i> sp. Gyrinidae <i>Orectochilus</i> sp. Psychomyiidae <i>Metalype</i> sp. Hydropsychidae <i>Hydropsyche</i> sp.
Coleoptera	Philopotamidae Rhyacophilidae <i>Rhyacophila</i> sp. Elmidae <i>Esolus</i> sp. <i>Limnius</i> sp. <i>Elmis</i> sp. <i>Gyrinus</i> sp. <i>Helichus</i> sp.
Diptera	Gyrinidae Dryopidae Dytiscidae Spercheidae <i>Spercheus</i> sp. Chironomidae Orthocladiinae Prodiamesinae Tanytarsini Tanypodinae Limonidae Ceratopogonidae Tabanidae Simuliidae Simuliini Empididae Clinocerinae Stratiomyidae Athericidae

correction for the cohort production interval (CPI = mean development time from hatching to final size; Benke 1979). We calculated the annual secondary production assuming a CPI equal to the minimum nymphal development period and also assuming a CPI equal to the maximum nymphal development period recorded in the studied population. We estimated nymphal biomass with the equation:

$$DM = a \cdot X^b, \tag{1}$$

or, in natural logarithmic form:

$$\ln(DM) = \ln(a) + b \cdot \ln(X) \tag{2}$$

where DM = individual dry mass, X = pronotum width, a = constant, and b = slope of the regression.

To construct the regression line, we measured 30 ethanol-preserved specimens, dried them at 60°C for 24 h, and placed them in a desiccator for 1 h. We weighed the dried specimens to the nearest 0.01 mg with a Sartorius Weighing Technology GmbH model MSE 125P-000-DA microbalance (Sartorius Weighing Technology, Gottingen, Germany).

Thirty nymphs of each sampling date, when possible, were processed to assess food consumption by means of two types of gut content analyses. For small individuals (< 15 mm total length), the contents of the alimentary canal were analyzed following the transparency method proposed by Bello and Cabrera (1999) and widely employed in stonefly feeding studies (e.g. Tierno de Figueroa, Sezzi, et al. 2003; López-Rodríguez et al. 2009): each nymph was singularly placed in a vial with Herwig's liquid for 24 h at 65°C, and afterwards, cleared individuals were placed in Herwig's liquid on a glass slide with a cover slip. For large nymphs (> 15 mm total length), guts were dissected and placed in Herwig's liquid on a glass slide with a cover slip, and afterwards analyzed. As previously observed, no differences resulted using both methods (Bo et al. 2008). Identifiable animal gut content items were sorted to the lower possible taxonomical level. For the remaining contents, five categories were used: (1) detritus, (2) CPOM (coarse particulate organic matter), (3) diatoms, (4) fungi, and (5) animal matter (unidentifiable animal remains > 1 mm). For all the categories, we estimated in percentage the area that they occupied in the guts.

Statistical analyses were performed using R (R Core Team 2014). For each category of gut content, mean, standard deviation and maximum-minimum were calculated. We also studied the correlation between size of the nymphs (measured as pronotum width) and percentage of the different gut contents by means of a Spearman R test.

Results

We collected 330 nymphs of *D. cephalotes* in 2004–2005 and 346 nymphs in 2012–2013. In both years, the life cycle was semivoltine with a total duration of two years, and so with nymphs of different cohorts coexisting at the same time (Figure 3a, b). Egg hatching was asynchronous, with small nymphs present in several months, so this hampers the exact estimation of nymphal development duration. Nymphal growth was slower in colder months, with nymphs of the biggest sizes recorded since January (in 2005) and November (in 2013), some of them even with black wingpads. Emergence took place at the end of April and, mainly, in May in both cases.

A total of 269 nymphs collected all through the year were used for the gut content analyses. Of them, 77 had the gut empty, while 192 had some kind of food in their guts (Table 2). The quantity of food inside the guts was highly variable, ranging from 5% to 100%. The nymphs behaved mainly as predators, feeding on different macroinvertebrate prey, but also included a lower quantity of detritus, CPOM and algae in their diets. Fungi and pollen grains were the scarcest items in the guts. Percentage prey significantly increased as the size of *D. cephalotes* nymphs increased, indicating that the biggest nymphs were more carnivorous

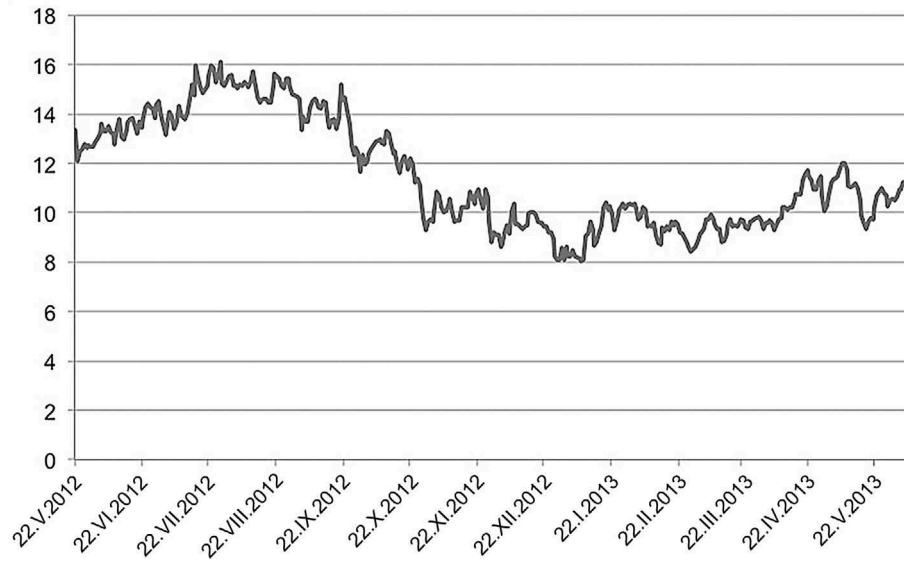


Figure 2. Mean daily temperatures during the study period in the Castril River.

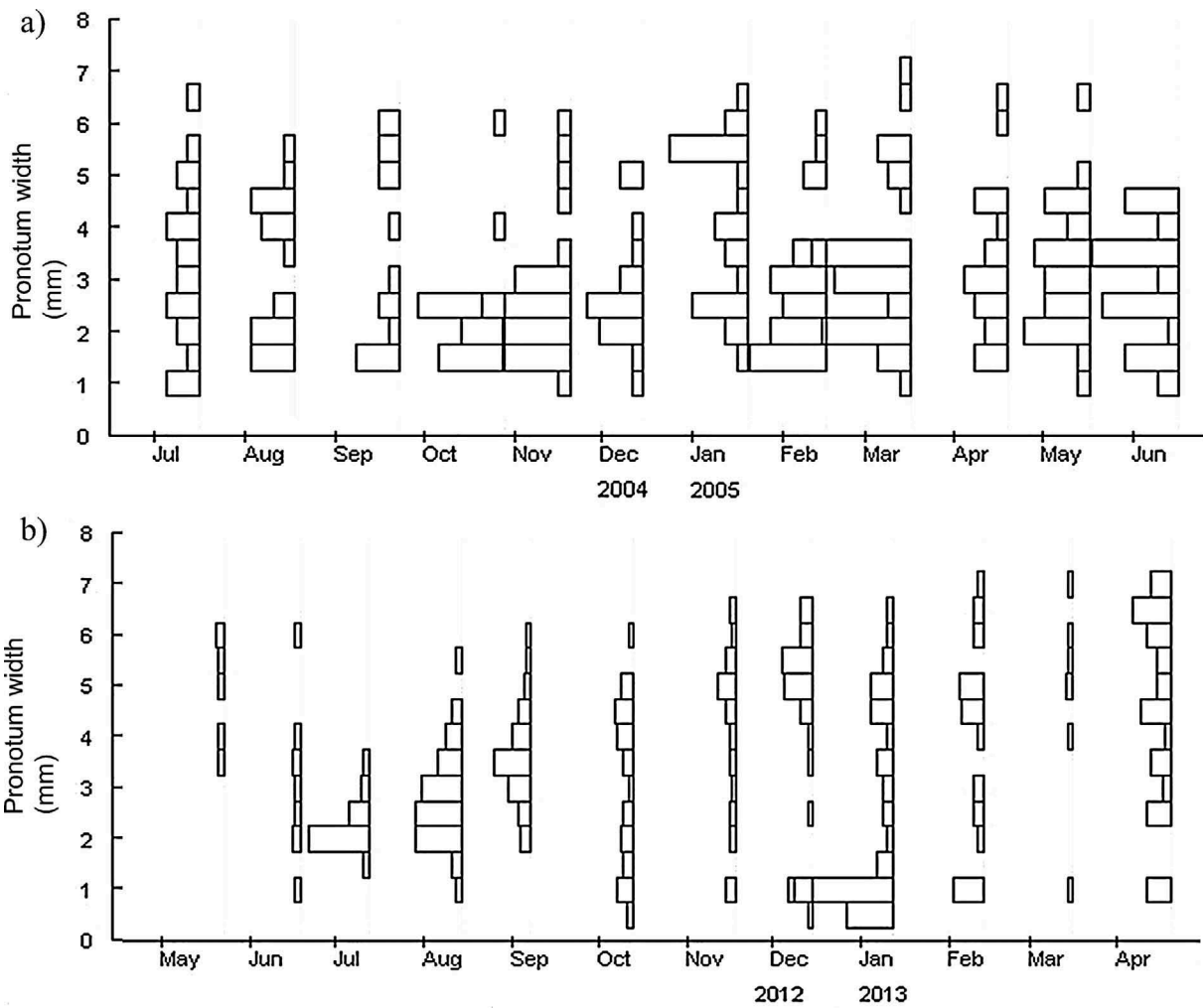


Figure 3. Life cycle of *D. cephalotes* in the study area in (a) 2004–2005 and (b) 2012–2013.

Table 2. Gut contents of *Dinocras cephalotes* nymphs in the Castril River, and results of the Spearman correlation test (*R*) between pronotum width and percentage of each item.

Items (%)	Mean	SD	Max	Min	<i>R</i>
Detritus	7.29	19.66	100	0	-0.56*
CPOM	3.70	10.64	100	0	-0.42*
Algae	2.63	10.46	70	0	-0.40*
Fungi	0.18	1.94	25	0	-0.01
Pollen	0.26	1.51	10	0	-0.25*
Prey	85.94	36.69	100	0	0.53*
<i>Baetis</i> sp. (Baetidae)	17.55	32.50	100	0	0.33*
<i>Serratella</i> sp. (Ephemerelellidae)	1.20	8.57	100	0	0.02
<i>Epeorus</i> sp. (Heptageniidae)	0.10	1.44	20	0	0.11
Ephemeroptera undet.	2.92	16.21	100	0	-0.01
<i>Leuctra</i> sp. (Leuctridae)	0.21	2.04	20	0	0.07
<i>Perla</i> sp./ <i>Dinocras</i> sp. (Perlidae)	0.68	7.52	100	0	0.12
Plecoptera undet.	0.99	8.66	100	0	0.05
<i>Micrasema</i> sp. (Brachycentridae)	0.16	1.61	20	0	0.14
<i>Sericostoma</i> sp. (Sericostomatidae)	0.63	7.35	100	0	0.17*
<i>Metalype</i> sp. (Psychomyiidae)	18.07	33.90	100	0	0.41*
<i>Hydropsyche</i> sp. (Hydropsychidae)	1.25	8.89	100	0	0.18*
Trichoptera undet.	1.25	10.36	100	0	0.01
Elmidae undet.	0.36	3.60	40	0	0.02
Prodiamesinae (Chironomidae)	11.69	28.72	100	0	-0.14*
Tanypodinae (Chironomidae)	1.35	10.30	100	0	-0.06
Tanytarsini, Chironominae (Chironomidae)	0.86	7.89	100	0	-0.08
Chironomidae undet.	5.52	20.51	100	0	-0.18*
Simuliidae	0.36	3.30	40	0	-0.05
Limoniidae	1.98	11.72	100	0	0.21*
Ceratopogonidae	0.63	7.35	100	0	0.11
Prey undet.	18.18	35.25	100	0	-0.00

*Significant at $p < 0.05$.

than the smallest, which ingested significantly more detritus, CPOM, algae and pollen (Table 2).

Regarding the ingested prey, Chironomidae (including Prodiamesinae, Tanypodinae and Tanytarsini), *Metalype* sp. (Psychomyiidae) and *Baetis* sp. (Baetidae) were the most important items in the nymphal diet of *D. cephalotes*. In general, the percentage of bigger prey (mainly Ephemeroptera, Plecoptera and Trichoptera) in the gut content increased as size of the nymphs increased. Thus, % Baetidae, % *Sericostoma* sp. (Sericostomatidae), % *Metalype* sp. (Psychomyiidae), % *Hydropsyche* sp. (Hydropsychidae) and % Limoniidae significantly increased as the size of *D. cephalotes* increased, while % Chironomidae decreased in the same situation.

In the studied population, dry weight (DW) of *D. cephalotes* was related to pronotum width (X) by the following equation:

$$\begin{aligned} \text{Ln DW} &= -1.57 + 3.12 \text{ Ln X} \\ (r^2 &= 0.94, F_{1,28} = 465.73, p < 0.05) \end{aligned} \quad (3)$$

The total biomass of the population was 744.90 mg m⁻², and the cohort production/biomass ratio was 6.39. We calculated the annual secondary production both assuming

a CPI of 20 months and a CPI of 14 months. In the first case, the annual secondary production was 2 854.46 mg DW m⁻² year⁻¹ and the annual production/biomass rate (P/B rate) was 3.83 year⁻¹. In the second case, the annual secondary production was 4 077.80 mg DW m⁻² year⁻¹ and the annual P/B rate was 5.47 year⁻¹.

Discussion

The life history of the studied population was similar in both studied periods, 2004–2005 and 2013–2014. In the study area, *D. cephalotes* behaves as a semivoltine species in contrast to what was reported by some other studies: e.g. Hynes (1941), Frutiger and Imhof (1991), Sánchez-Ortega and Alba-Tercedor (1991) and Iannilli et al. (2002) reported a life cycle of three years in the English Lake District, in a Prealpine Swiss river, in Sierra Nevada (Spain) and in an Appenninic river (Italy), respectively; Huru (1987) reported a life cycle of four to five years in Northern Norway, and Sand and Brittain (2001), also in Norway, reported a life cycle of five to six years. Nevertheless, our results coincide with the two year life cycle for *D. cephalotes* under a temperature similar to that of our study area suggested by Frutiger (1987). Moreover, the asynchronic egg hatching previously known for this

species (Zwick 1996a, 1996b), and also indirectly observed in our study from the almost continuous existence of small nymphs, means that the nymphal development period could be different among individuals, as reported by Sánchez-Ortega and Alba-Tercedor (1991). The studied population shows a slower growth in the colder period (winter), especially during the second year of the life cycle, with mature nymphs even from November in 2012, as noted by other authors (e.g. Sánchez-Ortega & Alba-Tercedor 1991). This could be due to the development of gonads and wingpads during the final instars (Frutiger 1996; Sand & Brittain 2001).

Throughout its distribution area, *D. cephalotes* is mainly considered a predator species, feeding principally on Chironomidae, Baetidae and some families of Trichoptera, and showing an ontogenetic shift in diet (metaphoetesis) from more detritivorous toward more predaceous habits (e.g. Berthélemy & Lahoud 1981; Lillehammer 1988; Lucy et al. 1990; Elliott 2003; Bo et al. 2007). In our study, this species presented a similar pattern, with Chironomidae, Psychomyiidae and Baetidae as the most important prey. Despite the wide trophic spectrum showed by this species, the comparison with previous results in the same river shows that the main prey remain the same in different years (Bo et al. 2008; López-Rodríguez et al. 2012).

Regarding secondary production of this species, to our knowledge, there is no available information throughout its distribution area, despite the importance of this parameter in understanding the fitness of populations (Benke 1993). A large difference exists between annual secondary production of this population considering a CPI of 20 or a CPI of 14 months. As mentioned before, there is an asynchronous egg hatching period in this species leading to differences in the development period among nymphs of the population, and this is shown by the different values of production. Thus, and taking into account that the emergence period is concentrated mainly in May, some nymphs would grow faster than others (those from eggs hatching in April in comparison with those hatching in October), and so they would produce more biomass per unit of area and time and they would have a higher annual P/B rate, but always within the most frequent interval reported by other authors (Waters 1977; Benke 1993). The annual P/B rates found in the population of *D. cephalotes* are comparable to those of other freshwater organisms with similar duration of the development period (see Huryn & Wallace 2000). On the other hand, the cohort P/B ratio is close to 5, which is the most frequent value for this parameter in aquatic insects (Benke & Huryn 2006).

If we compare our results with those of the other predator stonefly with semivoltine life cycle in nearby regions (*Guadalgenus franzi* [Aubert 1963] in López-Rodríguez et al. 2009) we observe that *D. cephalotes* has a greater annual secondary production, even when we consider a CPI

of 20 months, probably due to its higher size at maturity. Nonetheless, the annual P/B of *G. franzi* is, overall, higher, probably due to the fact it inhabits a temporal stream and so growth is faster and concentrated in the months when the stream has water. In a broader sense, annual secondary production of this population is higher than usually reported for predators, but the annual P/B is within the range of the most frequent values (Benke 1993).

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