Life history, feeding and secondary production of two Nemouroidea species (Plecoptera, Insecta) in a temporary stream of the Southern Iberian Peninsula

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With 5 figures and 4 tables

Abstract: We studied some ecological aspects of two taxa of Nemouroidean stoneflies (*Tyrrhenoleuctra* sp. and *Brachyptera vera cordubensis*) from a seasonal stream in Southern Europe. *Tyrrhenoleuctra* sp. shows a univoltine life cycle with a nymphal dormancy during the drought, and a long flight period. The eggs of this species are fully developed when laid, and hatch rapidly after laying, indicating a certain degree of ovoviviparism. The first instar nymph is described for the first time. In contrast, *B. vera cordubensis* shows a fast seasonal univoltine life cycle with an egg dormancy. The feeding behaviour study reveals that *Tyrrhenoleuctra* sp. can be catalogued mainly as a gatherer-collector while *B. vera cordubensis* can be classified mainly as a scraper, although neither of them belong solely to a single functional group. No significant changes are detected in the diet in relation to nymphal size, although larger individuals of *B. vera cordubensis* ingest more CPOM than small ones. Both taxa had similar biomass, but *B. vera cordubensis* had a higher secondary production and annual P/B rate.

Key words: *Tyrrhenoleuctra* sp., *Brachyptera vera cordubensis,* seasonal stream, life cycle, growth, trophic behaviour, secondary production.

Introduction

Nemouroidea constitutes a superfamily of Plecoptera including five families and more than 1500 species (Fochetti & Tierno de Figueroa 2008). The biology of this group has been studied mainly in permanent waters, where it shows a wide variety of life strategies. Species within this group have life histories ranging from multivoltine [e.g. *Nemurella pictetii* Klapálek, 1900] to merovoltine [e.g. *Pachyleuctra benllochi* (Navás, 1917)], though univoltine cycles dominate and include both fast seasonal and slow seasonal cycles. Feeding mechanisms are also diverse, with scraper, shredder and gatherer-collector species. The superfamily presents several interesting reproductive behaviours too and may include both oviparous or ovoviviparous species [the latter scarcer but cited, for example, in some *Capnia bifrons* (Newman, 1838) populations] (see Tierno de Figueroa et al. 2003a). The species that inhabit temporary streams have been less studied than those in permanent streams, even though the constraining characteristics of these environments may favour the development of particular strategies. Drought is a fundamental conditional factor in the growth and development of the aquatic insects that live in temporary rivers and streams (Giller & Malmqvist 1998). For example, fast seasonal life cycles with egg or nymphal dormancy periods, ovoviparity, eggs with

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membranes that resist drying, or asynchronous growth (reflected in high levels of adult polymorphism) are some of the strategies previously detected in temporary water species (Harper & Hynes 1970, Berthélemy 1973, Hynes 1976, Zwick 1980, Puig et al. 1990, Jacobi & Cary 1996). In the present study, we selected two taxa of Nemouroidea whose nymphal biology is almost completely unknown: *Tyrrhenoleuctra* cf. *minuta* (Klapálek, 1901) and *Brachyptera vera cordubensis* Berthélemy & Baena, 1984.

Tyrrhenoleuctra is a Western Mediterranean stonefly genus comprising a complex of species that recently has begun to be clarified despite the lack of morphological differences (Fochetti et al. 2004). In a recent article assessing the phylogenetic relationships among members of the *Tyrrhenoleuctra* genus, Fochetti et al. (2009) included populations from Sierra Morena (the mountain system where our study area is sited) within the *Tyrrhenoleuctra minuta*-complex. Nevertheless, as this complex has yet to be clarified, we will refer to this taxon as *Tyrrhenoleuctra* sp. throughout the text. Information on the biology of members of the genus *Tyrrhenoleuctra* is scarce. Different degrees of ovoviviparity and the existence of nymphal diapause have been reported for *T. tangerina* (Navás, 1922) and *T. minuta* (Berthélemy 1973). Data on nymphal feeding of several species of the genus show that *Tyrrhenoleuctra* is mainly detritivorous (Tierno de Figueroa et al. 2003b). Members of this genus usually inhabit temporary streams (including isolated pools), spanning from low (almost to sea level) to high altitude (1500 m a.s.l.) and its flight period lasts from the end of winter to spring, although it is variable (Tierno de Figueroa et al. 2003a).

Brachyptera vera Berthélemy & González del Tánago, 1983 is an endemic from the Iberian Peninsula that includes two subspecies, one of which, *B. vera cordubensis*, occurs in our study area. No data are available regarding the biology of this subspecies, except that a winter flight period has been confirmed (Tierno de Figueroa et al. 2003a).

Our aim is to increase the scarce knowledge on nymphal biology (life cycle, growth, feeding behaviour and secondary production) of both taxa living in a seasonal stream. These species were also chosen for being the most abundant Nemouroidea stoneflies in the stream. This information will also be useful for a better understanding of the adaptations of Nemouroidea species to this harsh habitat.

Material and methods

The study was conducted in Río Despeñaperros (Sierra Morena, Jaén, Spain; UTM: 30SVH558476, 560 m a.s.l.), a Mediterranean seasonal stream. We collected samples during the period when the stream carried water, and samples were collected midmonthly from November 2006 to May 2007, and biweekly in June, just before the summer drought. We did not detect any pools during the dry period. It was not possible to sample in mid April due to a flood caused by heavy rain, so the April sample was taken at the end of the month. The stream began to flow
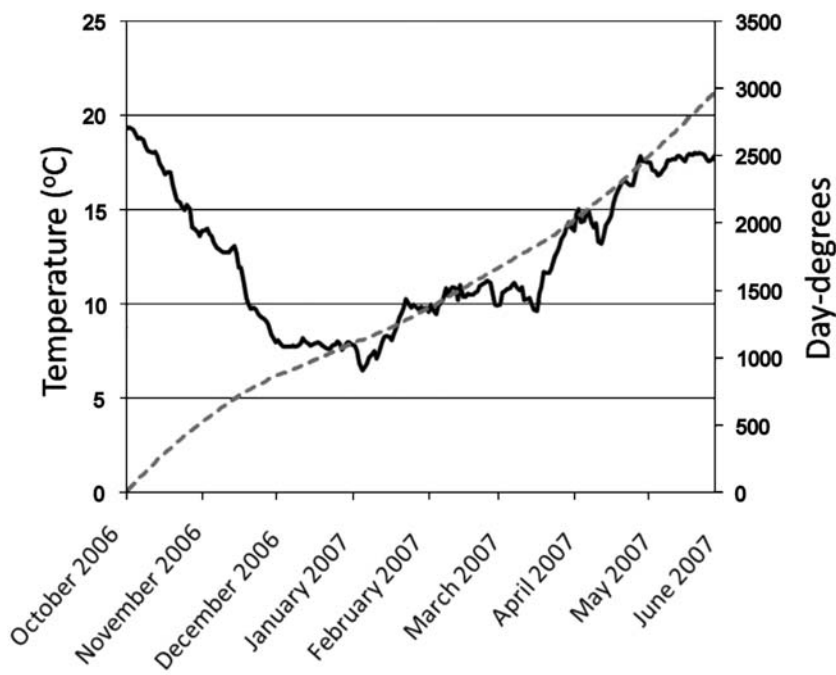
Fig. 1. Mean daily temperature (black line) and accumulated day-degrees above 0 °C (grey dotted line) during the wet period.

Table 1. Physicochemical parameters of the sampling site.

	N	Mean	S. D.	Minimum	Maximum
pH	9	8.24	0.34	7.61	8.79
Ammonium (mg/l)	9	0.65	1.84	0.00	5.55
Phosphates (mg/l)	9	0.01	0.01	0.00	0.03
Nitrates (mg/l)	9	0.03	0.04	0.00	0.11
Nitrites (mg/l)	9	0.04	0.05	0.00	0.13
Sulfates (mg/l)	9	22.55	7.26	10.14	33.24
Chlorides (mg/l)	9	49.10	8.70	36.40	68.25
Alkalinity (meq HCO_3^-/l)	9	39.85	7.86	24.64	50.02
Ss (mg/l)	9	4.02	4.17	0.60	12.60
Ca (mg/l)	9	65.96	12.80	50.40	88.00
Mg (mg/l)	9	29.70	7.77	20.90	40.34
Hardness (mg $CaCO_3$/l)	9	286.94	54.13	213.87	379.77
Turbidity (NTU)	9	1.33	0.87	0.40	3.20
O_2 (% sat)	9	69.11	23.75	13.00	92.00
O_2 (mg/l)	9	7.03	2.73	1.10	9.70
Temperature (ºC)	5908	12.54	3.86	5.90	25.87
Conductivity (µS/cm)	9	454.89	69.43	359.00	553.00
Discharge (m³/s)	9	0.10	0.11	0.00	0.32

at the end of October. A datalogger in the riverbed (HOBO® Water Temp Pro, 0.001 ºC accuracy) recorded the temperature hourly and temperature data were averaged for each day to produce mean daily temperatures (Fig. 1). Prior to the arrival of the water, the datalogger was exposed to the atmosphere and so the temperature recorded fluctuated widely. These fluctuations declined as water entered the stream enabling the beginning of the wet period to be established as October 23rd to 25th.

We recorded in situ physical parameters, such as dissolved oxygen, conductivity and discharge, each time samples were collected by means of an oxy-meter, a conductivity-meter and a flow-meter, respectively. We also collected one litre samples of water, these were chilled to approximately 4 ºC and transported to the laboratory for additional physicochemical analysis (Table 1). Analysis took place within 24 hours of sample collection.

This stream had a typical Mediterranean typology. Stream width during the sampling period varied from 2.95 to 5.35 m, and depth ranged from 0.04 to 0.31 m. The substrate was composed of approximately 85 % block and stones, 10 % gravels and 5 % sands and silt. There were some branches and trunks on the riverbed. During the spring and summer there were abundant Ranunculaceae and *Nasturtium* sp. Mosses were absent at the sampling site. Riparian vegetation was abundant and mainly consisted of *Nerium oleander*, *Fraxinus* sp., *Berberis* sp., Poaceae, Umbelliferae and Compositae.

We collected samples using a Surber sampler (0.09 m² area and 250 µm mesh size). In order to include the different meso-habitats, we took six replicates on each sampling date. Animals were preserved in 4 % formalin and brought to the laboratory, where they were sieved with a 150 µm mesh size sieve to remove excess formalin and fine detritus. Stoneflies were sorted and identified to species or morphospecies. Identification to species of individuals belonging to the genus *Tyrrhenoleuctra* was not possible because there are no morphological differences between species. Thus in this paper we refer to *Tyrrhenoleuctra* sp. All the individuals were counted and density of the

population was calculated by dividing the total number by the sampled area.

We measured total body length and pronotum width of 30 individuals each month using a micrometer inserted into the eyepiece of a binocular microscope (0.01 mm accuracy). Measures were standardized by putting every individual between two slides. As the two measures were highly correlated (Gamma correlation higher than 0.76 for every case, $p < 0.05$), we used total length for representing the life cycles of the studied taxa. Individuals were separated into 1 mm intervals. The size-frequency graphs representing the life cycles were made with FiSAT II software (Gayanilo et al. 2002).

Secondary production was calculated using the size-frequency method (Hynes & Coleman 1968, Hamilton 1969, Benke 1979, Benke & Huryn 2006). As a non-cohort method, its use is appropriate for populations where individual cohorts cannot be distinguished, and where nymphal size spread is high, as in our case. This method assumes that a mean size-frequency distribution determined from samples collected throughout the year approximates a mortality curve for an average cohort (Benke & Huryn 2006). Biomass (*B*) of each size class is calculated by multiplying density of individuals (*N*) by individual dry mass (*DW*), which is estimated according to the equation:

$$DW = a\,X^b$$

or, in natural logarithmic form:

$$\text{Ln } DW = \text{Ln } a + b\,\text{Ln}X$$

where *DW* = individual dry weight, *X* = total body length, *a* = constant, and *b* = slope of the regression. In order to evaluate the validity of the equation we employed an ANOVA analysis.

For estimating the regression equation, 30 formalin preserved specimens of each taxa were measured, dried at 60 ºC for 24 hours and placed in a desiccator for 1 hour. After this, they were weighed to the nearest 0.001 mg using a Mettler model M3 microbalance. Benke & Huryn (2006) stated that formalin preserved individuals provide estimates comparable

to those of nonpreserved specimens. Nevertheless weight loss due to preservative may result in a slight underestimate of the final results, as pointed out by some authors (e.g. Giberson & Galloway 1985).

The size-frequency method is based on the loss of biomass between two consecutive size classes over the life cycle or year. Biomass loss is calculated multiplying mass at loss [the mean value of the dry mass of two consecutive size classes, i.e., (DW_1 + DW_2)/2] by the reduction of density of individuals between two consecutive size classes (N of one size class minus N of the following size class, i.e., $N_1 - N_2$). The biomass loss between size classes is then multiplied by the total number of size classes, and summed in order to obtain the total production. We calculated the cohort P/B ratio (cohort production/biomass ratio) by dividing the total production by the biomass of the population (i.e., the sum of biomass of all the size classes). The biomass turnover or annual P/B rate (annual production/biomass rate) was calculated by dividing the production corrected by means of the cohort production interval (CPI, i.e. the mean development time from hatching to final size, Benke 1979) by the biomass of the population.

Stonefly diets were determined by observing the gut contents of stoneflies of different sizes. The diet study was performed according to the methodology used by Bello & Cabrera (1999), as in other studies of stonefly feeding (e.g. Tierno de Figueroa et al. 2006, López-Rodríguez & Tierno de Figueroa 2006, Navarro-Martínez et al. 2007, Fenoglio et al. 2009). Each individual was placed into a vial with Hertwig's liquid and heated in an oven at 65 °C for approximately 24 hours, enabling a clear view of gut contents. After this, specimens were mounted on slides for study under the microscope. We estimated the absolute percentage of gut content inside the digestive tract (at 40×) as the total area occupied by the content in the whole digestive system (from the mouth to the anus), and the relative gut content (at 400×) as the area occupied for each component within the total gut content, using a microscope with an ocular micrometer. The taxa were classified into functional feeding groups (FFG) according to food sources and mechanisms of

food acquisition (Cummins 1973, Merritt & Cummins 2006). We also studied the correlation between size of the nymphs and gut contents by means of a Gamma correlation test with STATISTICA software (Statsoft 2005).

During the sampling program, adults of the two taxa were collected by beating the vegetation with an entomological net and picking them directly from the stones. Some of these individuals were preserved in 70 % ethanol for establishing the flight period together with the information obtained from collection of mature nymphs. Some adults were brought alive to the laboratory and allowed to mate in pots in order to acquire egg clutches so that development could be assessed. Unfortunately, we only obtained clutches from *Tyrrhenoleuctra* sp. due to high adult mortality in *Brachypetra vera cordubensis*. Eggs thus obtained were maintained in Petri dishes with stream water at room temperature and development was assessed by viewing eggs under a microscope.

For statistical analysis, STATISTICA software (StatSoft 2005) was employed. Normality of each variable's distribution was assessed by means of a Kolmogorov-Smirnov test. None of the variables studied were normally distributed (Kolmogorov-Smirnov test, $p > 0.05$ in all cases), thus non-parametric statistics were used in all cases. A Gamma correlation test was used to test for an association between total length and protonum width, and size and percentage of the different components of the diet as there was a high degree of range overlap between variables (Guisande González et al. 2006).

Results

Río Despeñaperros had a relatively warm temperature regime, with temperature ranging from 5.90 °C to 25.87 °C during the wet period (Fig. 1, Table 1). During this time, the stream accumulated a total of 2962 day-degrees. Water chemistry and temperature patterns
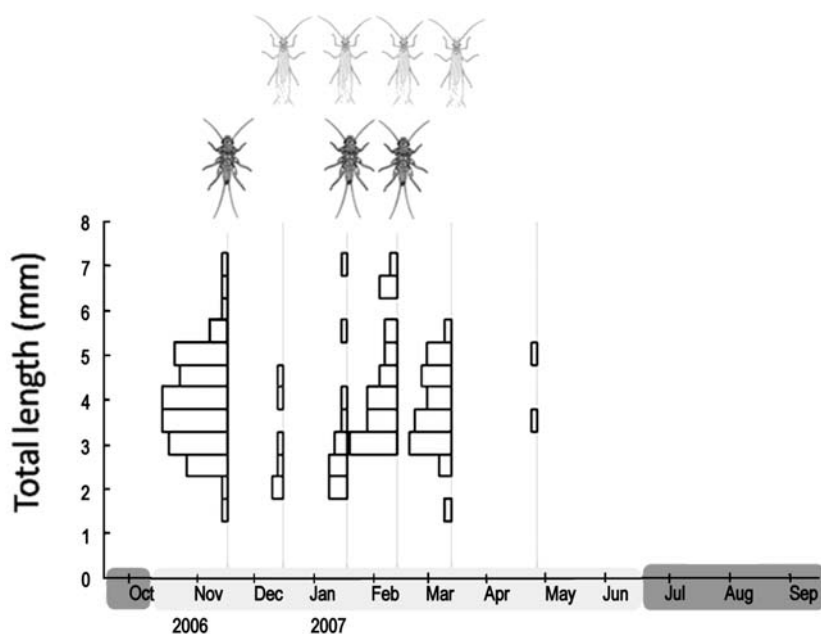
Fig. 2. Size-frequency graph representing the life cycle of *Tyrrhenoleuctra* sp. (N = 200). Mature nymphs are marked with a nymph drawing, and adults are represented by a macropterous adult draw. The period in which the stream was dry is marked darker in the horizontal axis.
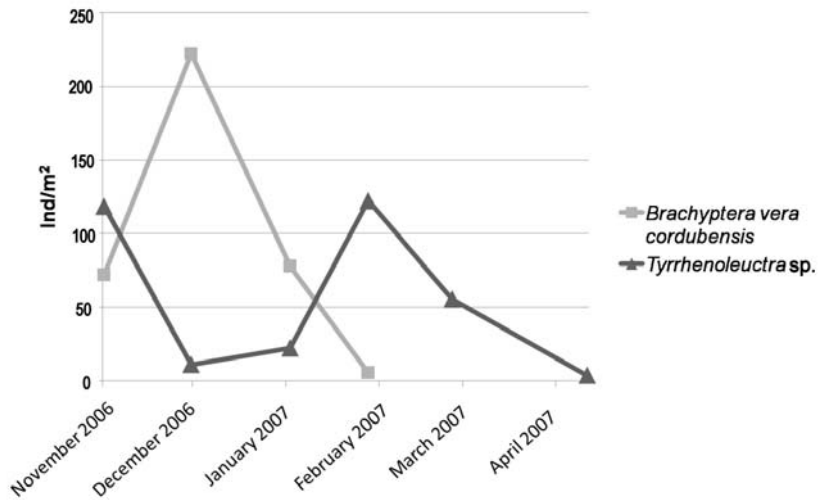
Fig. 3. Density of individuals of the studied taxa on each sampling date.

Table 2. Nymphal gut contents of the studied species in the sampling site. FFG = Functional Feeding Group.

Taxa		% absolute	% detritus	% diatoms	% hyphae	% fungi spores	% CPOM	% Cyano-bacteria	FFG
Tyrrhenoleuctra sp.	N	104	77	77	77	77	77	77	**Gatherer-**
	Mean	43.09	52.96	38.12	1.78	0.18	2.96	4.25	**collector/scraper**
	SD	30.08	31.92	32.71	8.08	0.48	6.28	13.49	
	Min-Max	0–100	0–100	0–98	0–70	0–2	0–40	0–90	
B. vera cordubensis	N	95	75	75	75	75	75	75	**Scraper/Gatherer-**
	Mean	32.89	25.91	65.48	0.33	0.03	0.99	7.12	**collector**
	SD	27.83	34.03	38.06	1.44	0.16	3.91	19.12	
	Min-Max	0–100	0–100	0–100	0–10	0–1	0–25	0–90	

were fairly typical of Mediterranean streams, with high conductivity but relatively low nutrient levels (Table 1). Some values related to the seasonal nature of the stream, such as the high ammonia (from breakdown of N-rich compounds during the dry period) or low oxygen in periods of low flow.

Life histories

We collected nymphs of *Tyrrhenoleuctra* sp. in the benthos from November to April, numbers were highest in November, just after the arrival of the water (Figs 2 and 3). Mature nymphs of *Tyrrhenoleuctra* sp. were present in November, just after water returned to the stream, and adults were seen in December. Early instar nymphs were also collected in November, before any eggs were seen, and there was a wide spread of nymphal body sizes during most sample dates. These data indicate that nymphs spend the dry period in a number of nymphal stages. The small nymphs present in December grew rapidly, and mature nymphs were seen again by January and February. Adults were collected

continuously from December to March, and no specimens were collected after the end of April. The size classes of nymphs collected in March were similar to those in the previous November, suggesting no growth during that period. In April few individuals were collected following a major flood and so it was not possible to examine size class patterns.

Microscope examination of two egg clutches from two female *Tyrrhenoleuctra* sp. showed that the nymphs were fully developed within the eggs, with distinguishable eyespots. After a few hours the eggs began to hatch, and first instar nymphs began to appear. They were unpigmented, had no ocelli, and possessed four cercal and nine antennal segments (Fig. 4). They had a low number of bristles in the union of every cercal segments. Interocelar distance was 0.12 to 0.13 mm, and total length was 0.47 to 0.77 mm.

Brachypetra vera cordubensis showed a more synchronous development pattern than *Tyrrhenoleuctra* sp. though there was still considerable variation in siz-
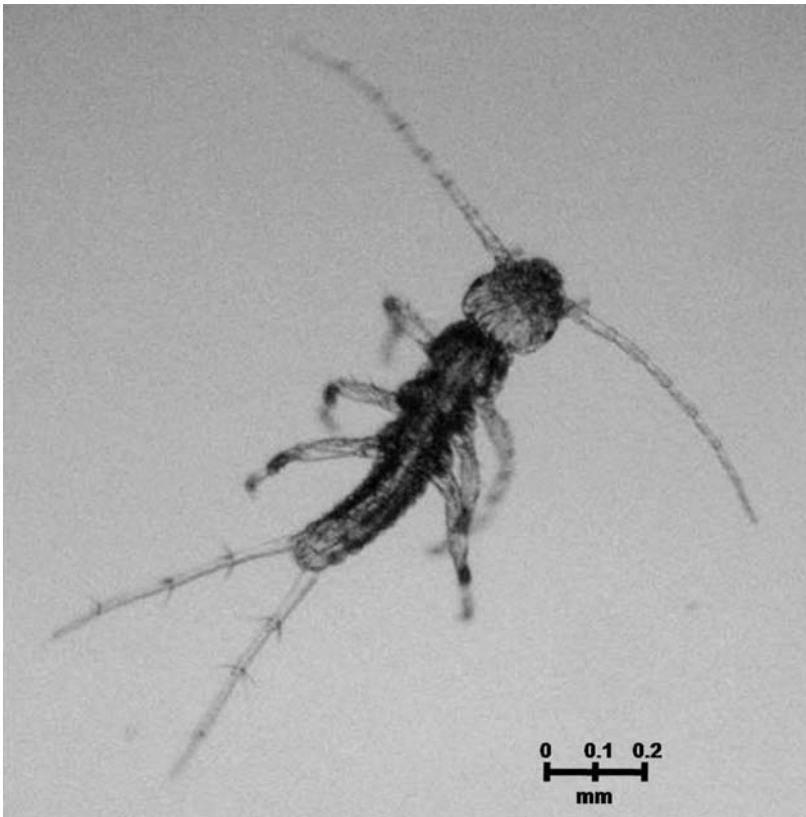
Fig. 4. First instar nymph of *Tyrrhenoleuctra* sp. (photograph of living individual).
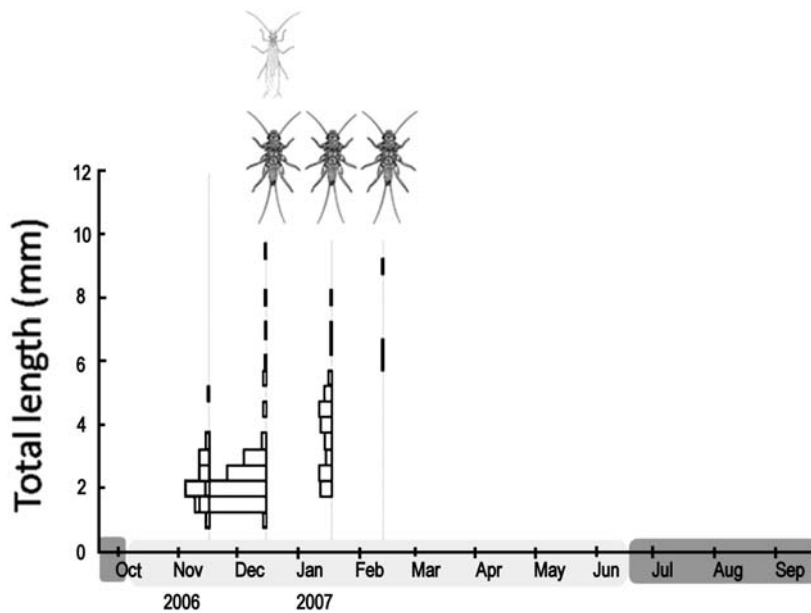
Fig. 5. Size-frequency graph representing the life cycle of *Brachyptera vera cordubensis* (N = 204). Mature nymphs are marked with a nymph drawing, and adults are represented by a macropterous adult drawing. The period in which the stream was dry is marked darker in the horizontal axis.

es on most sample dates. Nymphs were present in the benthos from November to February, with the maximum number of individuals in December, and very few in the last month (Figs 3 and 5). In November, only small nymphs were collected, but by December, numbers had increased and some mature nymphs and adults were seen. Mature nymphs were also found in January and February but no adults were seen at this time. The growth of this taxon was very fast. Mature nymphs of January and February were probably those of early instar nymphs seen in November and December (Fig. 5).

Feeding

When we analyzed the gut contents of the studied taxa we observed that both fed mainly on detritus and diatoms, detritus being most important in the diet of *Tyrrhenoleuctra* sp. and diatoms in the diet of *B. vera cordubensis* (Table 2). Thus, we can catalogue *Tyrrhenoleuctra* sp. as mainly a gatherer-collector, but also with an important role as a scraper. *Brachyptera vera cordubensis* was mainly a scraper, acting secondarily as a gatherer-collector. We found other components in the gut, such as Cyanobacteria, coarse particulate organic matter (CPOM) and fungal remains, but they were ingested less frequently.

Correlation between nymphal size and the percentage of each component found in the gut revealed that *Tyrrhenoleuctra* sp. did not experience changes in food intake pattern in relation to size (Gamma correlation non significant in any case, Table 3). Nonetheless, in *B. vera cordubensis* there was a positive correlation between size and percentage of CPOM found in the gut (Gamma correlation = 0.52, $p < 0.05$, Table 3), but no relationship between size and any other food component.

Secondary production

In the studied taxa, dry weight (*DW*) was related to body length (*X*) by the following equations:

Ln *DW* = −5.365 + 2.44 Ln*X*, ($r^2 = 0.89$, $F_{1,28} = 233.63$, $p < 0.05$) for *Tyrrhenoleuctra* sp.
Ln *DW* = −6.704 + 3.59 Ln*X*, ($r^2 = 0.82$, $F_{1,28} = 129.05$, $p < 0.05$) for *B. vera cordubensis*.

Table 3. Gamma correlations between total length and the percentage of the different food items in the studied taxa. Values marked with an asterisk are significant at $p < 0.05$.

	Tyrrhenoleuctra sp. total length (mm)	*B. vera cordubensis* total length (mm)
% detritus	−0.01	−0.07
% diatoms	0.02	0.02
% hyphae	0.16	0.04
% fungi spores	0.10	0.10
% CPOM	0.11	0.52*
% Cyanobacteria	0.00	0.06

Secondary production parameters of the studied taxa are summarized in Table 4. The annual secondary production of *Tyrrhenoleuctra* sp. was 26.10 mgDW m^{-2}year^{-1} and a total biomass of 263.17 mg/m^2. Therefore, the annual production/biomass rate (P/B rate) was 7.14 year^{-1}, and the cohort P/B ratio was 3.57. In contrast, *B. vera cordubensis* had an annual secondary production of 55.26 mgDWm^{-2}year^{-1}. The total biomass of this taxon was equal to 224.46 mg/m^2. Thus, the annual P/B rate was equal to 11.82 year^{-1} and the cohort P/B ratio equal to 7.20.

Discussion

Life histories

In the study area, *Tyrrhenoleuctra* sp. seems to show a univoltine life cycle, in which growth occurs mainly during the wet period, with a possible nymphal dormancy during the drought. We found first instar nymphs just hours after females released eggs, indicating the oviposition of embryonated eggs, as has been cited by Berthélemy (1973) for this genus. This same author pointed out that species belonging to the genus *Tyrrhenoleuctra* have a nymphal diapause, particularly after the fifth moult in *T. tangerina*. In our study area, some kind of dormancy would allow the nymphs to pass the spring and summer drought period in a resting stage, probably buried in the hyporheic zone. Support for this hypothesis can be found by comparing the size frequency distributions at the beginning and end of the drought period, which were very similar. The flight period during the wet period was extended for this species, occurring from December through to March, with recruitment occurring throughout the winter. Long flight periods (4–5 months in this case) and continuous recruitment periods are both strategies reported for temporary water fauna (Williams 2006) and would allow the survival of the population in case of an unpredictable drought (or flood, as was seen in the study stream in April). This strategy works well for species with mainly autumnal and/or winter flight periods, as with those studied in the present paper. The long flight period (and long period of oviposi-

Table 4. Secondary production parameters and densities of the studied species.

Species	Annual production (mgDWm^{-2}year^{-1})	Annual P/B (year^{-1})	Cohort P/B	Mean monthly density (ind./m^2)	Total density (ind./m^2)
Tyrrhenoleuctra sp.	26.10	7.14	3.57	55.56	333.33
B. vera cordubensis	55.25	11.82	3.94	94.44	377.78

tion) results in nymphs being in different stages of development when adverse conditions arrive (because no synchronization was detected). Thus, they go into dormancy with different sizes. Nymphal dormancy periods in different instars have been recorded for other stoneflies, for example *Capnia bifrons* usually undergoes dormancy (diapause) in the fourth or fifth instars, but sometimes in third, sixth or even seventh instars (Khoo 1964). *Tyrrhenoleuctra* sp. nymphs showed rapid growth during the wet period, completing development in only a few months.

In *B. vera cordubensis* we detected a fast-seasonal life cycle according to the classification of Hynes (1970). We collected a very high number of early stage individuals during November and December but by December, there were also mature nymphs and adults, either indicating extremely rapid growth, or suggesting that for some nymphs, nymphal development started some months before. From the presence of both mature nymphs and adults (although the latter were rarely collected) we can say that this taxon has a relatively long flight period of approximately three months from December through February. The lack of new recruits to the population during the winter months suggests that eggs remain in the stream until the beginning of the next wet period, probably in egg diapause. The presence of relatively large nymphs just after the resumption of flow indicates that some nymphs may also be in a dormant stage, as for the previous taxon. In Taeniopterygidae, nymphal diapause has been detected in the third, fourth, fifth or sixth instars (Harper & Hynes 1970). Because we did not collect small nymphs for several months before the arrival of the drought, it is more probable that the taxon has evolved to pass the drought in the egg stage. As pointed out by Hynes (1970), embryonic diapause in the egg stage is probably the easiest way that species can cope with drought. Furthermore, such a dormancy period has already been recorded for other species of *Brachyptera* (Khoo 1964, Harper & Hynes 1970, Neumann 1992). Egg diapause may have broken before the stream began to flow again with nymphs living in the hyporheic zone until the water table reached the surface following the arrival of rain. Though there was a great spread in the nymphal size, a cohort could be detected, corresponding to the one that finished its development in January and February. Thus, the growth of this cohort was extremely fast, taking approximately 4 months. Such a rapid growth has been also detected in other species inhabiting temporary streams, including some Taeniopterygidae species as *Brachyptera galeata* Koponen, 1949 (four months) (Alouf 1989)

or *Rhabdiopteryx christinae* Theischinger, 1975 (also four months) (López-Rodríguez & Tierno de Figueroa 2006).

Feeding

Tyrrhenoleuctra sp. behaved mainly as a gatherer-collector and this agrees with work done on other species in this genus by Tierno de Figueroa et al. (2003b), but also functioned as a scraper. Leuctridae are usually classified as shredders (Tachet et al. 1980) but because of the great quantity of diatoms ingested, it is not possible to assign this species to a single group since the presence of different types of food implies that no single feeding mechanism is involved (Stewart & Stark 2002).

Brachyptera vera cordubensis was mainly a scraper though gut contents showed that detritus was also important in the diet. Similar feeding patterns were found for other *Brachyptera* species in North Africa by Azzouz & Sánchez-Ortega (2000); this genus possesses a file-like structure for scraping stones (Hynes 1976). The proportion of CPOM in the diet of this subspecies increased as nymphs grew larger probably because of the higher shredding power of bigger nymphs with reinforced mandibles, though CPOM was never a major part of the diet. This subspecies would fit the category assigned to its entire family (Tachet et al. 1980) although, as in the previous case, the diet was too broad for any exclusive category to be assigned to it, as has been pointed out for Plecoptera in general by Stewart & Stark (2002).

Secondary production

The annual secondary production of *B. vera cordubensis*, the taxon with a shorter life cycle, is higher than that of *Tyrrhenoleuctra* sp., despite the fact that their biomass in the study site is not very different. This is also shown in the high value of the annual P/B rate of *B. vera cordubensis*.

Our values for annual secondary production and annual P/B rate of *Tyrrhenoleuctra* sp. do not differ from the range usually recorded for other Leuctridae species from European permanent waters (Krno 1996, Krno 1997, Krno & Šporka 2003), and are relatively low compared with other gatherer-collectors (Benke 1993). For *B. vera cordubensis* these values are lower than those reported for other Taeniopterygidae (e.g. Krno 1997). If we compare the value found here to those for other scrapers, the annual secondary production is within the range of most frequently found values (Benke 1993). Nonetheless, the annual P/B is

relatively high and uncommon for a scraper. Scrapers although they often feed on high quality food, generally do not have especially high P/B values, as many of them are relatively large (Benke 1993). In our study, the relatively high value of annual P/B could be a consequence of the small size of the species and its fast growth.

Conclusions

These two taxa present different strategies to cope with drought. *Tyrrhenoleuctra* sp. shows a certain degree of ovoviviparity, and passes the dry period in the nymphal stage, probably buried in the substrate and by means of a nymphal dormancy, whereas *B. vera cordubensis* spends it in the egg stage, with an embryonic diapause. Although the egg stage is more resistant to harsh conditions such as seasonal drying, nymphs have the capacity to move deep into the hyporheic zone, where the conditions may remain moist. The two studied taxa both showed a wide nymphal size spread, rapid growth and long autumnal/winter flight periods, typical strategies of temporary stream fauna. They both also showed a generalist condition in feeding. Their fitness to this environment is also supported by the values obtained in the secondary production analysis, that in the case of *B. vera cordubensis* is reflected in a high annual P/B rate. Therefore, this taxon would produce much biomass very quickly, as a consequence of a very high growth rate.

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