

LARVAL HABITATS AND LONGITUDINAL DISTRIBUTION PATTERNS OF *CORDULEGASTER HEROS* THEISCHINGER AND *C. BIDENTATA* SÉLYS IN AN AUSTRIAN FOREST STREAM (ANISOPTERA: CORDULEGASTRIDAE)

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From May 1997 to April 1998 larvae were recorded at the Weidlingbach, a fourth order tributary of the Danube nr Vienna, at 12 sampling stations from source to mouth. From the 14 larval instars reported for the genus, 5 (F to F-4; based on head width) could be identified in both spp.; head widths of ♀ larvae were significantly larger than in ♂. – Both spp. were most abundant within medium sand sediments with a mean grain size (Q_{50}) of 2.04 mm in *C. bidentata* and 2.79 mm in *C. heros*. Mean water depths and nose current speeds measured at larval microhabitats were 4.4 cm and 2.3 cm s⁻¹ (*C. bidentata*) and 5.6 cm and 2.6 cm s⁻¹ (*C. heros*). During the winter months larvae chose the water depths slightly deeper than during summer. Throughout the observation period, a high proportion of the larvae (*C. bidentata*: 70-100%; *C. heros*: 41-90%) were burrowed in sandy sediments, either totally or displaying the typical ambush posture with only head and anal pyramid visible. In winter, the proportion of burrowing larvae was insignificantly higher than in summer. – *C. bidentata* larvae were most abundant near the sources, preferring first order stream sections (discharge 0.1-3.21 s⁻¹) with high hardness (up to 34 German degrees) and conductivity (up to 1100 μS cm⁻¹) and a high proportion of fine sediments. Although *C. heros* larvae were also collected at such first order sites, they reached their highest abundance (larval density up to 7.84 specimens per 10 meter shore length) at second order stream sections (discharge 0.3-6.01 s⁻¹) with lower hardness and conductivity and a higher proportion of coarse sediments.

INTRODUCTION

With respect to wingspan and body length, *Cordulegaster heros* Theischinger is the largest European Odonata species (ASKEW, 1988). Despite this, its distribution patterns and ecology are largely unknown. This is undoubtedly a consequence of frequent taxonomic changes within this genus. A member of the „*boltoni* complex“, *C. heros* was classified as *C. boltonii charpentieri* (Kolenati) by ST. QUENTIN (1952). This

decision was doubted by JURZITZA (1965), who shared FRASER's (1929) opinion in that the taxon in question required a species rank and, consequently, renamed it *C. charpentieri* (Kolenati) (synonym = *C. pictus* Sélys). Finally, in 1979, the taxon was described as *C. heros* by THEISCHINGER with nominate form based on type material from the Wienerwald area near St. Andrä (Lower Austria) and *C. h. pelionensis* based on material from Mt Pelion (Greece). In contrast to *C. heros*, *C. bidentata* has retained its name since its first description in 1843 as *C. bidentatus* Sélys.

In the Weidlingbach catchment, *C. bidentata* and *C. heros* are syntopic and easy to identify as larvae and adults (ASKEW, 1988; HEIDEMANN & SEIDENBUSCH, 1993; THEISCHINGER, 1979). Although details on life cycle, biology and ecology of *C. bidentata* and *C. boltonii* are available (e.g. PRODON, 1976; BLANKE, 1984; BUCHWALD, 1988; DONATH, 1988; DOMBROWSKI, 1989; SALOWSKY, 1989; BÖCKER, 1995; BISSINGER, 1996; CORBET, 1999), this is not yet the case in *C. heros*. In addition, it is well known that *C. boltonii* and *C. bidentata* may colonize the same stream (e.g. BÖCKER, 1995; LAISTER, 1996a), whereas niche differentiation patterns of syntopic populations of *C. boltonii* and *C. heros* are still unknown. The aim of the present study was, therefore, to provide information on micro- and longitudinal distribution of these species, to elucidate abiotic parameters responsible for the observed distribution patterns and to work out habitat templates for *C. bidentata* and *C. heros*.

STUDY AREA

The study was carried out at the Weidlingbach, a 12-km-long, first to fourth order tributary of the Danube. Its drainage area (33.2 km²) is situated in the Wienerwald, the densely forested easternmost

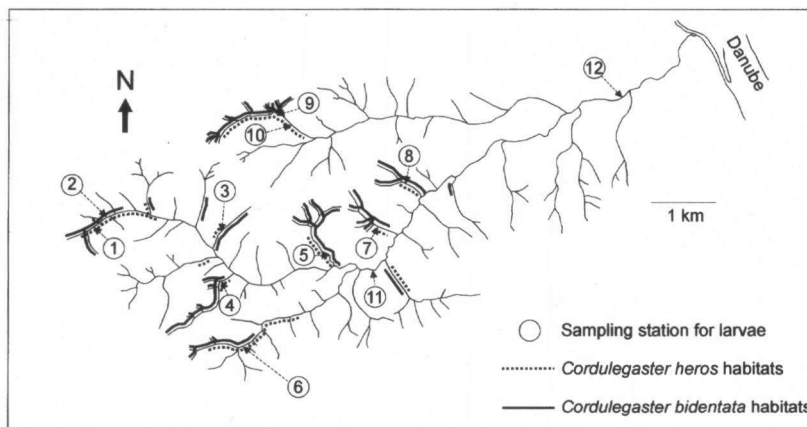


Fig. 1. The Weidlingbach catchment near Vienna, Austria, showing the habitats of *Cordulegaster heros* and *C. bidentata*. The pooled data are based on surveys of adults, larvae and exuviae (LANG, 1999; MÜLLER, 1999). The twelve sampling stations are indicated by encircled numbers.

spur of the Alps near Vienna, Austria (Fig. 1; 48°17' N, 15°16' E; altitude of source: 440 m; altitude of mouth: 164 m above sea level). Near the source, mean stream width is 2.1 m and maximum water depth 16 cm, near the mouth 3.9 m and 71 cm, respectively. The chemical properties of the water are heavily influenced by the calcareous sandstone, marl and slate geology, producing relatively high conductivity (480-1100 $\mu\text{S cm}^{-1}$) and total hardness (up to 34 German degrees). Annual pH values range from 6.6 to 8.4, and the oxygen content is always well above 80%. The range of annual water temperatures is 0.0-18.0°C at first order and 0.5-20.0°C at fourth order stretches of the stream (DIETRICH & WARINGER, 1999).

The catchment was mostly covered by deciduous forest consisting of *Fagus sylvatica*, *Carpinus betulus*, *Quercus* spp. and *Acer* spp.; only the lower reaches of the brook were bordered by human settlements. Sandy substrates were common within first and second order tributaries, but cobbles and pebbles predominated in the lower reaches. The mean annual discharge of first order tributaries was 0.002 m^3s^{-1} ; near the mouth it increased to 0.2 m^3s^{-1} , but may be as high as 7.2 m^3s^{-1} during spates due to the poor infiltration capacity of the soil (HADL et al., 1976).

MATERIAL AND METHODS

For the investigation of larval habitats, 12 data sets were collected at monthly intervals between May 1997 and April 1998 at 12 sampling stations (Fig. 1) and over a wide range of hydrological conditions (except severe spates where sampling was impossible). Each sampling station covered a stream section 10 m in length. At each sampling date, maximum and minimum stream width was recorded, the water depth read at a gauging station and the stream section mapped. Discharge was measured using a propeller-meter (Ott C2; propeller diameter = 30 mm) and following the principles of the velocity-area method (DINGMAN, 1984). Water temperature data were read from permanently-exposed minimax-thermometers; in addition, hardness and conductivity were measured at monthly intervals using Aquamerck field kit No. 8039 and a microprocessor conductivity meter (WTW LF 196), respectively.

For larval sampling, each station was surveyed thoroughly and repeatedly for two hours in an upstream direction („catch per unit effort“), using a hand net (18 cm diameter, mesh size = 1 mm). Information on the microhabitat of each individual larva was obtained by recording the following parameters: water depth from the tarsus of the larva's fore leg up to the water surface to the nearest mm using rulers; larval position within the stream bed; riffle or pool situation; direction of the larva with respect to water flow; larva burrowed or at the sediment surface. Subsequently, larvae were transferred individually into coded plexiglas boxes and the larval position within the stream bed was marked by a tiny coded flag. Water velocity acting at larval positions („nose current velocity“) was measured using the propeller-meter in its downmost position and correcting these velocity data according to the body height of the larvae, using dimensionless diagrams for uniform turbulent flow given by DINGMAN (1984). At extremely shallow locations (water depth < 60 mm), drops of potassium permanganate were released by means of a pipette at a depth corresponding to the larva's height, enabling the determination of the travelling time of the colour cloud over a given distance (= 10 cm) using a stopwatch. After species and sex were identified, head width, length of wing sheets, mentum diameter, tibial length and total length were measured to the nearest 0.1 mm in the field with callipers.

In order to obtain information on substrate composition, sediment samples (= 1.5 dm^3) were taken at larval locations, dried in an oven to constant weight and sieved using a sieving machine (Retsch VS 1000) with mesh widths ranging from 20 μm to 20 mm.

The statistical packages SPSS 6.0 for Windows and STATISTICA for Windows were used for statistical analysis.

RESULTS

LARVAL INSTARS

From May 1997 to April 1998 a total of 688 *Cordulegaster heros* and 314 *C. bidentata* larvae were collected. Based on frequency distribution histograms of head

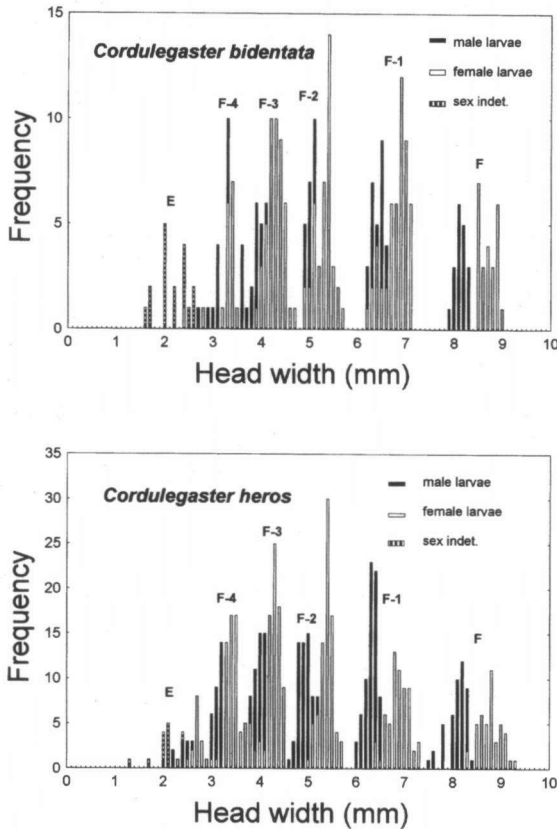


Fig. 2. Frequency distribution histograms of head width measurements (male and female larvae; early instars whose sex could not yet be identified) of *Cordulegaster bidentata* (n = 314) and *C. heros* (n = 688). Instar numbers are marked at the top (E = early instars).

width measurements we were able to identify the instars F to F-4 (Fig. 2) from the 14 instars reported for the genus. In addition, a small number of larvae younger than F-4 was collected. In both species, biometric parameters within a given instar such as head width (Fig. 2), total length, wing sheet length, tibial length, mentum width and mentum length were consistently greater in female larvae. Instar grouping for both species was checked by correlating each larval instar number with its ln-transformed mean head width, yielding highly significant regressions. The proportion of the variance of head width due to the regression of head width on instar number was ≥ 0.99 in all cases.

In *C. heros*, on two sampling dates and in *C. bidentata*, on four sampling dates (from a total of 12 dates) the sex ratio of larvae was significantly different from 1:1 (χ^2 test; $P > 0.05$), showing an excess of female larvae. Based on exuviae (n = 91), however, the sex ratio in both species was not significantly different from equality.

LARVAL LIFE CYCLE

The instar composition of larval samples for each month is shown in Table I. At a given sampling date, several instars per species could be collected simultaneously. In June, larval samples consisted mostly of instars F-3, F-4 and earlier instars in *C. heros*; this peak shifted to F-1 to F-3 instar larvae in December. In April, the penultimate and in May the ultimate instar larvae were most abundant. In June, the proportion of final instar larvae decreased significantly, indicating the emergence period which started in late May and lasted until early July. Instar distribution in *C. bidentata* roughly followed the same pattern (Tab. I).

MICROHABITAT CHARACTERISTICS

Both *Cordulegaster* species clearly preferred small sediment grain sizes (Fig. 3), this trend being even more pronounced in *C. bidentata*. For example, 71.7% of the latter species was collected in fine, medium and coarse sand substrate (grain size =

Table I

Life history data of *Cordulegaster heros* and *C. bidentata* in the Weidlingbach from May 1997 to April 1988, showing the proportion (%) of larvae within a given instar (F, F-1, F-2, F-3, F-4; E = early instars). Total numbers of larvae collected at each month are given in brackets. For both species, emergence took place from late May until early July

<i>Cordulegaster heros</i>												
	May (100)	Jun (105)	Jul (43)	Aug (95)	Sep (98)	Oct (73)	Nov (28)	Dec (25)	Jan (24)	Feb	Mar (33)	Apr (64)
F	29.0	9.5	2.3	9.5	10.2	15.1	10.7	4.0	20.8		15.2	15.6
F-1	23.0	13.3	4.7	7.4	22.5	26.0	32.1	36.0	20.8		21.2	40.6
F-2	9.0	9.5	30.2	29.5	29.6	23.3	32.1	28.0	29.2		36.7	17.2
F-3	6.0	23.8	27.9	25.3	25.5	20.6	17.9	20.0	16.7		21.2	18.8
F-4	21.0	27.6	30.2	29.0	8.2	8.2	3.6	4.0	8.3		6.1	7.8
E	12.0	16.3	4.7	9.5	4.1	6.9	3.6	8.0	4.2			
<i>Cordulegaster bidentata</i>												
	May (38)	Jun (64)	Jul (23)	Aug (60)	Sep (40)	Oct (30)	Nov (11)	Dec (4)	Jan (9)	Feb	Mar (7)	Apr (28)
F	15.8	3.13	26.1	16.7	12.5	20.0	9.1		22.2		28.6	10.7
F-1	50.0	26.6	17.4	13.3	7.5	20.0	27.3	25.0	55.6		42.9	35.7
F-2	7.9	18.8	13.0	28.3	22.5	13.3	18.2		11.1		14.3	28.6
F-3	15.8	37.5	21.7	15.0	35.0	20.0	9.1	75.0	11.1		14.3	17.9
F-4	7.9	12.5	17.4	15.0	12.5	16.7	9.1					7.1
E	2.6	1.6	4.4	11.7	10.0	10.0	27.3					

0.063-2.0 mm), but only 60.8% of *C. heros* larvae. On the other hand, 35.4% of *C. heros* larvae inhabited fine, medium and coarse gravel (grain size = 2.0-63 mm), but only 23.6% in *C. bidentata*. In stony substrate (grain size > 63 mm) the proportion of both species was 0.6%. In addition, 4.1% of *C. bidentata* and 3.2% of *C. heros* larvae were associated with particulate organic matter. Differences of Q_{50} -means of the two *Cordulegaster* species were highly significant (t and F-test; $P < 0.001$).

Nose current speeds (= water velocities corrected for upper body edge) at larval locations ranged from 0 to 11 cm s^{-1} (Fig. 3), with up to 38.2% of *C. bidentata* larvae

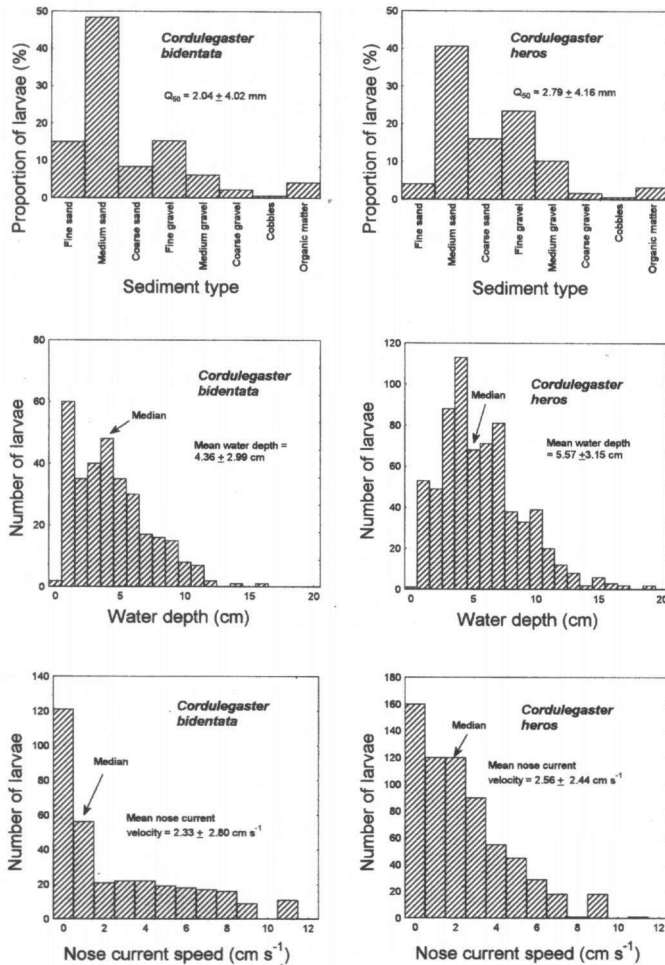


Fig. 3. Sediment type, water depth and nose current speed preference histograms of *Cordulegaster bidentata* (n = 314) and *C. heros* (n = 688). In the inserts, data are given as means (or median grain size Q_{50}) \pm S.D. Current speed data are corrected according to the maximum body height of larvae (= "nose current speed"), using dimensionless diagrams for uniform turbulent flow given by DINGMAN (1984).

and up to 23.3% of *C. heros* larvae collected at completely stagnant microhabitats. In the former species, the mean nose current velocity was 2.33 cm s^{-1} , in the latter species 2.56 cm s^{-1} , and these differences were highly significant ($P < 0.01$; log+1)-transformation and subsequent t-test for comparing means and F-test for comparing variances).

Over a whole hydrological year, water depth at larval positions ranged from less than 1 cm up to 20 cm in *C. heros* and up to 16 cm in *C. bidentata* (Fig. 3). The mean water depth at the spots of *C. bidentata* larvae over the year was 4.4 cm, for *C. heros* larvae 5.6 cm. The means were highly significantly different ($P < 0.001$; t-test for comparing means and F-test for comparing variances). Negative correlations between water depths of larval locations and water temperature were observed (Fig. 4).

During the observation period, a high proportion of the larvae of both species (*C. bidentata*: 70-100%; *C. heros*: 41-90%; Fig. 5) were burrowed in fine sediments, either totally or displaying the typical ambush posture with only head and anal pyramid visible. Only few larvae were positioned on the sediment surface, uncovered. Although not significant ($P > 0.05$; Spearman's rank correlation coefficient), more larvae of both species were collected within the sediments in winter than in summer (Fig.5).

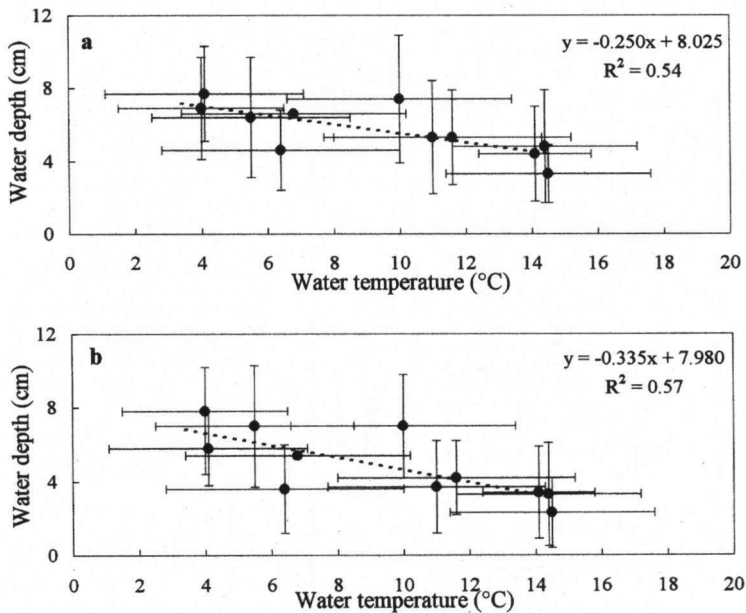


Fig. 4. Relationship between water temperature (°C) and water depth preferences (cm) of larvae of (a) *Cordulegaster heros* and (b) *C. bidentata*. Data are given as monthly arithmetic means \pm S.D. Dots: regression lines. The regression equations were highly significant; coefficients of determination are shown in the upper right inserts. Each mean is based on 24-100 data in (a) and 4-64 data in (b).

LONGITUDINAL ZONATION PATTERNS

In order to detect longitudinal zonation patterns of environmental variables which might be responsible for the spatial distribution patterns observed in the Weidlingbach catchment, a principal component analysis of site-specific abiotic data listed in Table II was made. According to the Kaiser criterion, three factors displayed eigenvalues > 1 ; however, the third eigenvalue was close to the limit of 1 and we therefore retained only two factors. As expected, the analysis revealed high factor loadings for parameters associated with Strahler stream order (= factor 1), such as stream width, water depth, discharge, coarse sediment proportion and maximum water temperature, but also for dissolved oxygen. The second factor yielded high loadings for hardness and conductivity (Tab. II). Therefore, the set of abiotic parameters measured at each sampling site could be reduced to a pair of variables representing the two factors. Differences in larval abundance between first and second stream order sites were highly significant ($P = 0.001$) in *C. bidentata* (mean

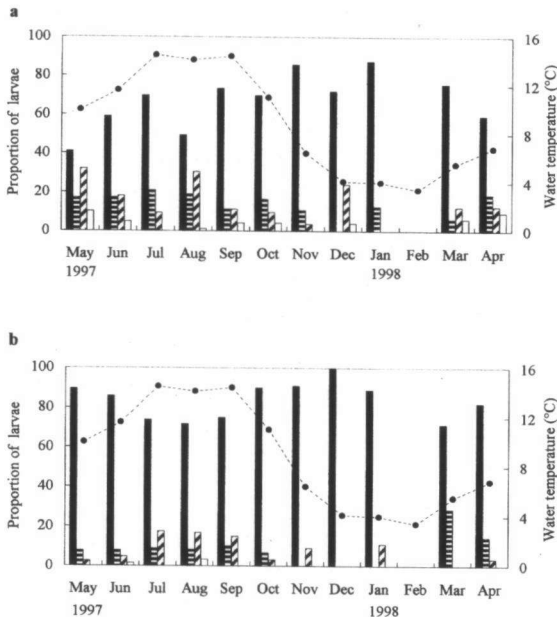


Fig. 5. Positions of larval locations, a: *Cordulegaster heros* (n = 688); b: *C. bidentata* (n = 314) in the Weidlingbach watershed. — [Black = burrowing larvae; — striped = larvae at sediment surface, heavily covered by sediment; — diagonally striped = larvae at sediment surface, slightly covered by sediment; — blank = larvae at sediment surface, uncovered by sediment particles; — monthly arithmetic means of water temperatures are indicated by black dots]

larval density per 10 m shore length 4.1 versus 2.3), but not significant ($P > 0.05$) in *C. heros* (7.8 versus 6.2 larvae per 10 m shore length; Kruskal-Wallis ANOVA). Differences between second and third/fourth order sites were significant ($P = 0.007$) in both species (mean larval density per 10 m shore length 2.3 versus 0.0 in *C. bidentata* and 6.2 versus 0.0 in *C. heros*). Based on the analyses above, *C. bidentata*-sites within the Weidlingbach catchment are situated close to the sources of the main stream and its tributaries, offering a high proportion of fine sediments; due to the proximity to springs and their close contact with the calcareous sandstone and marl of the soil, the water is

Table II

Factor loadings of abiotic parameters at the twelve larval sampling sites as obtained from a principal component analysis with two factors (1 and 2) extracted and varimax rotation. Loadings > 0.7 are underlined

Abiotic parameters	Factor 1	Factor 2
Minimum stream width (m)	<u>0.894</u>	0.136
Maximum stream width (m)	<u>0.756</u>	0.297
Maximum stream depth (m)	<u>0.975</u>	0.015
Annual minimum water temperature (°C)	0.390	-0.576
Annual maximum water temperature (°C)	<u>0.809</u>	0.018
Annual minimum discharge (m ³ s ⁻¹)	<u>0.943</u>	0.038
Annual maximum discharge (m ³ s ⁻¹)	<u>0.961</u>	0.038
Annual minimum dissolved oxygen (mg l ⁻¹)	-0.041	-0.343
Annual maximum dissolved oxygen (mg l ⁻¹)	<u>0.723</u>	0.206
Percentage of coarse sediment (pebbles, cobbles)	<u>0.970</u>	0.108
Strahler stream order	<u>0.884</u>	0.275
Annual minimum hardness (German degrees)	-0.186	<u>-0.940</u>
Annual maximum hardness (German degrees)	-0.156	<u>-0.957</u>
Annual minimum conductivity (µS cm ⁻¹)	-0.091	<u>-0.960</u>
Annual maximum conductivity (µS cm ⁻¹)	-0.068	<u>-0.964</u>

very hard (up to 34 German degrees), with conductivity values up to 1100 µS cm⁻¹. Such habitat templates are typical for first order streams where stream width is approximately 2.5 m, water depth approximately 27 cm and discharge < 3.2 l s⁻¹. On the other hand, typical *C. heros* sites are of second stream order with stream width up to 3.4 m, water depth up to 30 cm and discharge of up to 60.0 l s⁻¹. At such locations, conductivity and hardness values are generally lower than at *C. bidentata* sites, reflecting their increasing distance from the sources. Whereas first order sites may be classified as excellent for *C. bidentata* and second order sites as excellent for *C. heros*, the abundance at „fair“ locations was significantly lower in *C. bidentata* and only insignificantly in *C. heros* (Tab. III).

DISCUSSION

From the six European *Cordulegaster* species (ASKEW, 1988), three are reported from Austria: *C. boltonii* (Donovan) and the two species studied in detail in the present study. Among the latter, *C. bidentata* inhabits mountainous regions in Spain, France, Belgium, Germany, central Europe as well as eastern Europe, the Balkan and Italy (ASKEW, 1988). In Austria, it is known from all nine federal states (LAISTER, 1996a, 1996b; LÖDL, 1976; PUSCHNIG, 1930; RAAB & CHWALA, 1995; STARK, 1976; THEISCHINGER, 1971). According to BUCHWALD (1988), *C. bidentata* is abundant at shadowy, calcareous spring locations (hardness = 13.8-20.6 German degrees, conductivity 330-460 µS cm⁻¹, pH = 7.1-8.2) within dense wood vegetation where larvae inhabit fine sediments at shallow microhabitats

(BLANKE, 1984; ROHN, 1992; VOLKER, 1955). This was also observed in the present study: *C. bidentata* clearly preferred first order stream sections close to the sources where discharge was $\leq 3.2 \text{ l s}^{-1}$, the slopes were steep (up to 150‰) and the proportion of small sediment grain sizes (e.g. medium sand, grain size = 0.2-0.6 mm) was high. Due to the soil geology and the short distance to the source, hardness and conductivity values were high (up to 34 German degrees and up to $1100 \mu\text{S cm}^{-1}$). The third Austrian species of this genus, *C. heros*, is known from eastern Austria (Lower Austria, Styria, Burgenland and Carinthia (MÜLLER, 1999; RAAB & CHWALA, 1995; RESSL, 1983; ST. QUENTIN, 1952, 1957; STARK, 1981a, 1981b; THEISCHINGER, 1976), Hungary (AMBRUS, 1992), Slovenia (KOTARAC, 1997), Croatia and Greece (THEISCHINGER, 1979). Generally, *C. heros* inhabits running waters at lower altitudes and in the lowlands. In the Weidlingbach basin, this species preferred second order tributaries with discharge ranging from 0.25 to 6.0 l s^{-1} , where slopes were not so steep (approximately 50‰) and the proportion of fine sediments was significantly lower than in first order stream sections. Due to the deposition of calcium carbonate upstream, hardness and

Table III

Ranking of sampling sites 1 - 12 (excellent, fair or poor breeding locations) based on larval densities of *Cordulegaster heros* and *C. bidentata* within the Weidlingbach catchment. Larval densities at sampling sites of first and second stream order were highly significantly different in *C. bidentata* ($n = 120$; Kruskal-Wallis-ANOVA, $p = 0.001$) but not significantly different in *C. heros* ($n = 120$; $p > 0.05$). Differences between second and third/fourth stream order sites were highly significantly different for both species ($p = 0.007$)

Parameter	Breeding habitat quality		
	excellent <i>bidentata</i> / <i>heros</i>	fair <i>bidentata</i> / <i>heros</i>	poor <i>bidentata</i> / <i>heros</i>
Mean larval density (n per 10 m shore length \pm 95% C.L.)	4.13 \pm 1.20 /	2.27 \pm 1.39 /	0.0 / 0.0
Annual range of maximum water depth (cm)	7.84 \pm 2.26 6-27 / 8-30	6.16 \pm 2.00 8-30 / 6-27	35-70 / 35-70
Annual range of water temperature (°C)	0.0-18.0 / 0.0-18.0	0.0-18.0 / 0.0-18.0	0.5-20.0 / 0.5-20.0
Annual range of discharge (l s^{-1})	0.1-3.2 / 0.3-6.0	0.3-6.0 / 0.1-3.2	7.5-195.0 / 7.5-195.0
Annual range of total hardness (German degrees)	17.0-34.0 / 16.4-28.0	16.4-28.0 / 17.0-34.0	17.0-22.0 / 17.0-22.0
Annual range of conductivity ($\mu\text{S cm}^{-1}$)	545-1100 / 480-909	480-909 / 545-1100	620-760 / 620-760
Annual range of stream width (m)	0.15-2.47 / 0.51-3.40	0.51-3.40 / 0.15-2.47	1.24-9.25 / 1.24-9.25
Strahler stream order	1 / 2	2 / 1	3-4 / 3-4
Sampling sites	P1, P3, P7, P8, P9 /	P2, P4, P5, P6, P10 /	P11, P12 /
	P2, P4, P5, P6, P10	P1, P3, P7, P8, P9	P11, P12

conductivity values were also lower (up to 26 German degrees and up to 909 $\mu\text{S cm}^{-1}$) at typical *C. heros* sites. Despite these different preferences, centres of maximum abundance of both species were linked by long stretches of stream bed where *C. bidentata* and *C. heros* were syntopic, although at reduced densities. Stream stretches inhabited by both species correspond to the „salamander region“ proposed by THIESMEIER (1992), where fish are lacking and *Salamandra s. salamandra* L. reaches its abundance peak (BAUMGARTNER et al., 1999). At such locations, firesalamander larvae and *Cordulegaster* species act as top predators, utilizing the same food items and preying on each other. Although *Cordulegaster* larvae are occasionally classified as cold-stenotherms (e.g. DITTMAR, 1955), they generally are very tolerant to higher water temperatures up to 18°C (present study) or even more than 20°C in southern France (SCHÜTTE, 1997); they may perhaps better be described as cold-adapted eurytherms (BUCHWALD, 1988).

Over the year, mean larval densities at excellent breeding locations were 4.13 larvae per 10 m shore length in *C. bidentata* and 7.84 larvae per 10 m shore length in *C. heros* (Tab. III). Maximum larval densities were observed in June (*C. bidentata*; 36 larvae per 10 m shore length) and in September (*C. heros*; 32 larvae per 10 m shore length). These observations match data given by DONATH (1988) for *C. boltonii* (20 larvae per 10 m shore length) and ROHN (1992) (1.5-10.7 larvae per 10 m shore length). Investigations by DOMBROWSKI (1989), SALOWSKY (1989) and BISSINGER (1996) yielded 2-5 specimens per 0.09 m², 6-52 larvae per m² and 10-29 specimens per CPUE hour, respectively. Generally, *Cordulegaster* larvae favour microhabitats situated in shallow, lentic stream sections (BUCHWALD, 1988; DONATH, 1988). This was also the case in the present study, where 78% of *C. bidentata* larvae and 69% of *C. heros* larvae were collected near the banks and away from the main current. As preferred food items are *ad libitum* throughout the stream bed of typical *Cordulegaster* habitats (DOMBROWSKI, 1989), the reduced water flow and the abundance of fine sediments near the banks most probably creates this distribution pattern. Of the two species studied in detail, *C. bidentata* larvae preferred slightly lower mean nose current speeds than *C. heros* larvae (2.3 and 2.6 cm s⁻¹, respectively; corrected for the upper body edge). Recorded maximum nose current speeds were 11 cm s⁻¹ for both species. Given as mean current speeds measured at 40% depth, the corresponding means were 4.0 and 4.3 cm s⁻¹, respectively (maximum: 21 cm s⁻¹). These values are in the lower range of current speeds reported by BUCHWALD (1988) for larvae of *C. bidentata* (10 cm s⁻¹) and *C. boltonii* (11-15 cm s⁻¹), by DONATH (1988) for *C. boltonii* (15-30 cm s⁻¹) and by FERRERAS ROMERO (1988) for the same species (6-100 cm s⁻¹).

Preferred water depths at larval locations ranged from 0-16 cm (mean = 4.4 cm) in *C. bidentata* and from 0-19 cm (mean = 5.6 cm) in *C. heros*. BUCHWALD (1988) observed water depths of 2-150 cm at brooks inhabited by *C. boltonii* and of 2-20 cm at streams where *C. bidentata* larvae were abundant. In addition, we recorded a negative correlation between water temperature and water depth of larval locations,

which can be interpreted as an avoidance of freezing since ice blocks first develop in shallow waters.

Other workers agree in that *Cordulegaster* larvae clearly prefer small sediment grain sizes (sand to medium gravel fraction; approximately 0.02-10 mm) and/or detrital deposits (e.g. BÖCKER, 1995; DOMBROWSKI, 1989; DONATH, 1988; KOTARAC, 1997; PRODON (1976); SALOWSKY, 1989; SCHMIDT, 1986). This was also the case in the present study, where 40-50% of both species preferred medium sand (0.2-0.6 mm; Fig. 3). Within this category, however, the median grain size (Q_{50}) was significantly lower in *C. bidentata* (2.04 mm) than in *C. heros* (2.79 mm). Differences of habitat sediment grain sizes are also reported for *C. boltonii* (0.016-0.3 mm) and *C. bidentata* (0.022-0.74 mm; BOCKER, 1995). When comparing substrate preferences of different instars within the Weidlingbach basin, small larvae clearly preferred large patches of fine sediments where heterogeneity was low, whereas large larvae were frequently collected at patches with high substrate heterogeneity, e.g. rather small sandy patches surrounded by coarse gravel particles, cobbles and stones.

Throughout the observation period, 70-100% of *C. bidentata* and 41-90% of *C. heros* were burrowed in fine sediments, either totally or displaying the typical ambush posture with only head and anal pyramid visible. Even moultings were observed to take place within the sediments. Therefore, both species may be classified as „shallow burrowers“ sensu CORBET (1999). Larvae removed from the substrate took only 1-2 minutes to regain their former ambush posture by digging with mid- and hindlegs as well as the abdomen. During the winter months, the proportion of burrowing larvae was generally higher in both species, and *C. heros* larvae were found up to 4 cm deep in the sediments. This was also observed in *C. bidentata* (ROBERT, 1959), whereas DOMBROWSKY (1989) did not detect any differences in borrowing behaviour between winter and summer. BÖCKER (1993), BUCHWALD (1988) and HEIDEMANN & SEIDENBUSCH (1993) agree that collecting *Cordulegaster* larvae is especially difficult in winter, perhaps because in winter larvae burrow even deeper than 10 cm. Burrowing postures may be also a function of sediment grain size; PRODON (1976) observed that *C. boltonii* larvae were almost completely covered by sediments within fine grain sizes (<0.125-0.25 mm), whereas they were almost completely uncovered and at the sediment surface within coarse grain sizes of 8 mm. Besides being useful for ambushers using optical and tactile stimuli (HEYMER, 1973), the burrowing behaviour of *Cordulegaster* larvae may also increase drift resistance and may be helpful in hiding from predators such as firesalamander larvae.

The sex ratio of exuviae was not significantly different from equality in *C. bidentata*, and *C. heros*, although a marked excess of female larvae could be observed on 4 sampling dates in the former and on two dates in the latter species. An excess of females has been also observed in Lestidae, Gomphidae (SUHLING & MÜLLER, 1996) and in the genus *Cordulegaster* (DONATH, 1988); this is probably because

resources may be better utilized by the bigger female larvae (intraspecific competition). Differences in head width between sexes were observed from the final instar back to instar F-5 or F-6 (Fig. 2). Significant differences in size between sexes was also observed in *C. boltonii* by ROHN (1992). At emergence, sex ratios range from 30.7-72.4 in Gomphidae, 38.9-52.7 in Corduliidae, 46.5-64.4 in Aeshnidae and 39.5-49.2 in Libellulidae (CORBET & HOESS, 1998).

Throughout the year, several larval instars could be collected simultaneously in *C. bidentata* and *C. heros*, reflecting the overlap of cohorts due to the long larval development in this genus. DOMBROWSKI (1989) reported 14 instars (prolarva not included) in *C. bidentata* and VERSCHUREN (1991) observed the same number of instars in *C. insignis* Schneider. In *C. bidentata*, instars 9-13 cease growth in the winter months, and the penultimate instar undergoes diapause development which is induced by longday conditions (DOMBROWSKI, 1989), providing a synchronisation mechanism for emergence.

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